Mill Creek Fisheries Monitoring Program: Ten Year Report. Final Report to Save-the-Redwoods League

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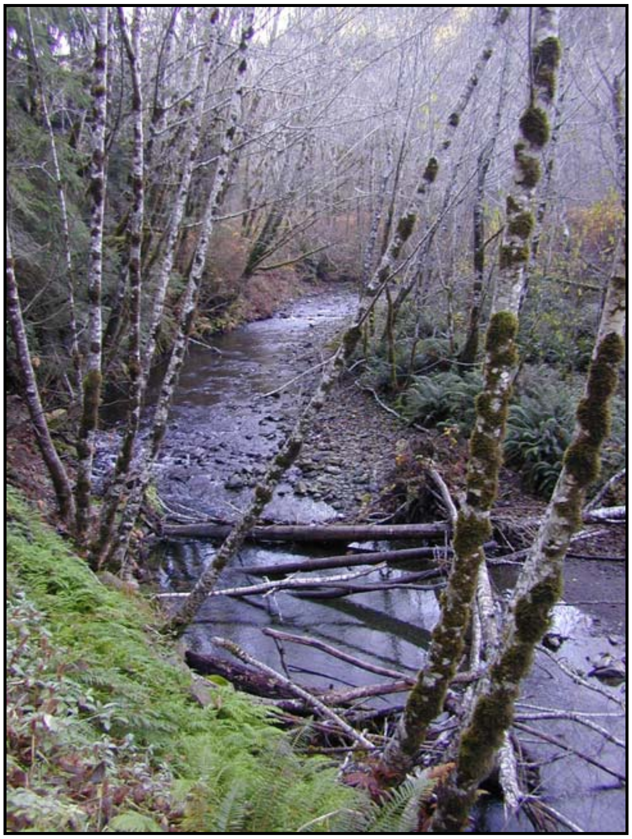

Mill Creek Fisheries Monitoring Program: Ten Year Report

Final Report

Prepared for
Department of Fish and Game
and
Save-the-Redwoods League

Prepared by
Stillwater Sciences
Arcata, California

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Executive Summary

Introduction

Coho salmon (*Oncorhynchus kisutch*) in the Southern Oregon/Northern California Coasts (SONCC) Evolutionarily Significant Unit (ESU) were listed as federally threatened in 1997 (NMFS 1997), which was reaffirmed on June 28, 2005 (NMFS 2005). In 2002, the California Fish and Game Commission issued a finding that coho salmon warranted listing as a threatened species in the SONCC ESU and as an endangered species in the Central California Coast ESU, directing the California Department of Fish and Game to develop a recovery strategy (CDFG 2004). Chinook salmon in the Southern Oregon and northern coastal California ESU were not warranted for federal listing (NMFS 1999).

Mill Creek is a tributary to the Smith River, the only major undammed river in California, and supports anadromous populations of coho salmon, Chinook salmon, steelhead, and coastal cutthroat trout. Population modeling was used to evaluate limiting factors for coho and Chinook salmon and prioritize restoration actions in the East Fork and West Branch of Mill Creek, the two main tributaries that join to form the mainstem Mill Creek, using data from a long-term fisheries monitoring program.

The primary objectives of this report were to build and parameterize population models for coho and Chinook salmon, evaluate existing data in the context of this modeling effort, identify potential limiting factors, and prioritize restoration alternatives and future monitoring efforts. A secondary objective was to predict coho salmon adult returns through the construction and use of a state-space model.

Methods

The conceptual models provide a foundation for the quantitative models by describing how we think the population functions and what we think are the relative importance of different sources of mortality for the population dynamics of the species. Two quantitative population models were developed for the Study Area: one for coho salmon and one for fall Chinook salmon. The models were developed in spreadsheet form using Microsoft Excel 2003®. The models follow the stock-production approach to population modeling, which is supported by a large body of literature spanning several decades (e.g., Paulik 1973, Moussalli and Hilborn 1986). The utility of these models, like all models, is constrained by the quality of the data that is used to populate them, and in some cases models may be best used to identify additional information needs. Nonetheless, the models represent a compilation of all available data, in a rigorous and transparent framework.

All available data on coho salmon and Chinook salmon in the East Fork and West Branch of Mill Creek was compiled to construct quantitative models. The models were used to determine the factors affecting both populations. The intention of the models was not to predict the precise population size of any particular life-stage, but rather identify critical life stages, and prioritize restoration actions and future monitoring efforts.

The Study Area includes: (1) the mainstem Mill Creek downstream of West Branch and East Fork Mill Creek; and (2) West Branch Mill Creek and East Fork Mill Creek upstream to natural fish passage barriers. West Branch and East Fork Mill Creek sub-watersheds were intensively managed for commercial timber harvest until recent acquisition and incorporation into the California State Park system (Stillwater Sciences 2002).

Results

The coho salmon population model is sensitive (>10% change in spawner abundance) to overwinter carrying capacity, summer rearing habitat carrying capacity, late summer survival, and overwinter survival. Our conceptual model hypothesized that rearing habitat, particularly overwintering habitat, would limit the current population, which is supported by model results. Doubling overwintering habitat in both tributaries increased the adult population size by more than 15%. Increasing summer rearing habitat has less of an impact on the population given the current parameter values than increasing overwintering habitat (for the West Branch, a 24% increase in the adult population size when doubling the habitat, as compared to a 45% increase when doubling overwintering habitat).

Within the model, decreasing overwinter and late summer survival in the West Branch given current conditions has an impact on the coho salmon population (12% decrease in equilibrium population size), although the change is not dramatic if marine survival is high enough to produce enough returning adults to fully seed the overwintering habitat. Model runs with marine survivals more typical of pre-water year (WY)[1] 2000 conditions (assumed to be 0.006, based on OPI marine survival indices from Chilcote et al. 2006) indicated that a 50% decrease in any one of the density-independent survival rates would lead to extinction.

For Chinook salmon, the model is sensitive to spring rearing carrying capacity, and not other freshwater parameters. The Chinook salmon conceptual model hypothesized that spring rearing habitat would limit the current population, which is also supported by model results. Doubling spring rearing habitat in both tributaries increased the adult population size by more than 40%. These values provide the relative magnitude in population change with respect to potential habitat changes. Increasing spring rearing habitat in the West Branch has slightly more value (55% increase) to the total population than increasing spring rearing habitat in the East Fork (45% increase).

Models for both species were sensitive to smolt to adult survival rates. The survival from smolt to adult parameter was only included to allow the population model to estimate escapement and predict equilibrium conditions. However, the influence of this parameter indicates the importance of smolt-to-returning-adult survival in the coho salmon and Chinook salmon life-cycles. This could have important implications for the Mill Creek salmon population in years with poor ocean conditions and low marine survival rates.

Recommendations

We recommend a continuation of the existing sampling methodologies of outmigrant trapping and juvenile abundance snorkel surveys, to evaluate any changes in carrying capacity that result from future management actions. Juvenile abundance snorkel surveys in the East Fork are also recommended to better define coho salmon summer carrying capacity, a sensitive model parameter, and improve our understanding of population dynamics in the East Fork. In addition, we recommend winter juvenile abundance snorkel surveys before and after winter freshets to help better quantify overwintering carrying capacity, the most sensitive freshwater model parameter for coho salmon.

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[1] Water year describes the 12 month period from 1 October to 30 September; the numeric designation is consistent with the calendar year in which it ends (i.e., WY 2005 is from 1 October 2004 to 30 September 2005).

Redd counts were useful in obtaining spawning escapement estimates, and future counts are recommended. Minimum escapement estimates involved a fair amount of subjectivity and are not adequate for population monitoring.

More accurate estimates of spawning escapement are needed for the state-space model to better predict adult returns. Weir counts could potentially be used to establish a relationship between the total numbers of spawners and redd counts to improve both past and future estimates for spawning escapement.

Population modeling identified overwintering habitat as the limiting factor for coho salmon populations, and we recommend that increasing overwintering habitat be the highest priority for any restoration activities. Large woody debris enhancements could potentially help increase overwintering habitat as well as summer rearing habitat.

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1 INTRODUCTION

Pacific salmon (*Oncorhynchus* sp.) have undergone a notable decline in population numbers, with habitat degradation and loss being major causes (Nehlson et al. 1991). Coho salmon (*Oncorhynchus kisutch*) in the Southern Oregon/Northern California Coasts (SONCC) Evolutionarily Significant Unit (ESU) were listed as federally threatened in 1997 (NMFS 1997), which was reaffirmed on June 28, 2005 (NMFS 2005). This ESU includes all naturally spawned populations of coho salmon in coastal streams between Cape Blanco, Oregon and Punta Gorda, California as well as three artificial propagation programs. In 2002, the California Fish and Game Commission issued a finding that coho salmon warranted listing as a threatened species in the SONCC ESU and as an endangered species in the Central California Coast ESU, directing the California Department of Fish and Game to develop a recovery strategy (CDFG 2004). Chinook salmon in the Southern Oregon and northern coastal California ESU were not warranted for federal listing (NMFS 1999).

There is primary interest in evaluating factors that may limit these populations, particularly for listed coho salmon, and for prioritizing restoration actions. Population modeling is a tool that can be used to conduct both of these tasks. This report summarizes our efforts to examine population dynamics of coho salmon and fall Chinook salmon (*O. tshawytscha*) in the Mill Creek watershed by developing a multi-stage stock-production model.

Mill Creek is a tributary to the Smith River, the only major undammed river in California, and supports anadromous populations of coho salmon, Chinook salmon, steelhead, and coastal cutthroat trout. The Mill Creek watershed (60 km^2 [23 mi^2]) includes the two main tributaries, the East Fork Mill Creek (East Fork, 20.5 km^2, 7.9 mi^2) and the West Branch Mill Creek (West Branch, 19.6 km^2, 7.6 mi^2) that join to form the mainstem Mill Creek (Stillwater Sciences 2002). The focus of this report is on coho salmon primarily, and Chinook salmon secondarily, in the East Fork and West Branch of Mill Creek.

Although ocean conditions can be the dominating factor in terms of coho abundance, as it was in the 1970's and 1980's (Coronado and Hilborn 1998), freshwater habitat conditions are also critical to the viability of coho salmon populations. Freshwater habitat conditions can play a major role in the interannual variability in numbers of outmigrating smolts (Bradford 1995). During years when ocean survival is especially low, if freshwater habitat conditions are poor, smolt production may not be high enough to ensure continuation of the run. By using population modeling, we can look at the various factors affecting the coho salmon population in freshwater and the ocean, and how each factor affects the population as a whole.

The primary objectives of this report were to build and parameterize population models for coho and Chinook salmon, evaluate existing data in the context of this modeling effort, identify potential limiting factors, and prioritize restoration alternatives and future monitoring efforts. A secondary objective was to predict coho salmon adult returns through the construction and use of a state-space model.

1.1 Modeling Approach

Our population models are essentially quantified conceptual models, organized around the principle of identifying and separating density-dependent and density-independent factors affecting the population. The level of detail of these models should not overrun the real scientific understanding of coho and Chinook salmon ecology. Several life stages were used to represent the life-cycles of fall Chinook and coho salmon, typically using two parameters per life stage. The detail and complexity of biological and biological-physical interactions were reflected in the development of suitable values for model parameters, rather than calculated within the model itself. These parameters were assigned values based on the existing dataset from Mill Creek and existing scientific literature where appropriate.

Initially, conceptual models were developed to provide a narrative description of the potential density-dependent and density-independent factors affecting each life stage of coho and Chinook salmon. Linkages were explored between changing habitat conditions and the population response for specific life stages, first in conceptual models, and then followed by quantitative assessment using multi-stage stock-production population models.

The stock-production approach is based on a large body of literature going back several decades (e.g., Paulik 1973). The model itself is a relatively simple and transparent spreadsheet (i.e., not a black box). The models will be made available to CDFG and Save-the-Redwoods League.

The model development process was intended to help determine which of the many gaps in our present understanding most impair our efforts to protect or enhance the population. Not all potential mechanisms need to be understood to the same level of detail, and not all system parameters need to be known to the same degree of accuracy. For all parameters, the model will be run for a range of values to determine the sensitivity of the model to these inputs. Based on the quality of available information, modeling some components of the population (e.g., coho pre-smolts and smolts in the West Branch) may be based on a full time series of data, whereas other areas (e.g., coho pre-smolts in the East Fork Mill Creek) may be based on more limited data.

Classically, a stock-production relationship is used to describe a complete life-cycle (e.g., to express the adult population of one generation as a function of the adult population of the previous generation). However, the idea can also be applied to specific life stages. We can identify a sequence of landmarks in the life-history, and step from each to the next with a stock-production relationship (Paulik 1973). Construction and examination of a multi-stage stock-production model for a population is essentially a limiting factors analysis, in which the interactions between potentially limiting factors are taken into account and examined.

The value of decomposing the overall stock-production relationship into a sequence of stage-to-stage relationships is that we may be able to relate the parameters of these individual relationships fairly directly to the biology of the animal modeled. In particular, we can attempt to break up the life-cycle in such a way that the r and K parameters of the individual stock-production relationships correspond to a partition of the factors affecting the population into density-independent and density-dependent terms, respectively, having fairly clear biological interpretations. For example, factors such as fecundity, or the dependence of egg survival on the quality of spawning gravels, are (at least to a first approximation) independent of population densities. Such factors will contribute to r terms. Factors such as abundance of overwintering habitat will contribute to K terms.

We attempted to use state-space modeling to further describe the coho salmon population in Mill Creek. State-space modeling is a tool which incorporates both population dynamics processes (the state process) and data collected from samples of the population (the observation process) (Buckland et al. 2004). This approach allows for incorporation of stochastic variation, as well as the incorporation of functions which relate population parameters to environmental variables. We used state-space models to predict adult escapement and to improve estimates of escapement using the complete time series of data collected in Mill Creek.

1.2 Study Area

The Study Area includes: (1) the mainstem Mill Creek downstream of West Branch and East Fork Mill Creek; and (2) West Branch Mill Creek and East Fork Mill Creek upstream to natural fish passage barriers (Figure 1). West Branch and East Fork Mill Creek sub-watersheds were intensively managed for commercial timber harvest until recent acquisition and incorporation into the California State Park system (Stillwater Sciences 2002).

In addition to coho salmon and fall Chinook salmon, chum salmon (*O. keta*), steelhead (*O. mykiss irideus*), coastal cutthroat trout (*O. clarki clarki)*, western brook lamprey (*Lampetra richardsoni*), Pacific lamprey (*Lampetra tridentata*), coastrange sculpin (*Cottus aleuticus*), prickly sculpin (*Cottus asper*), threespine stickleback (*Gasterosteus aculeatus*), and Klamath smallscale sucker (*Catostomus rimiculus*) (Albro and Gray 2002) are known to occur in the Study Area.

2 METHODS

2.1 Conceptual Model

The conceptual models provide a foundation for the quantitative models by describing how we think the population functions and what we think are the relative importance of different sources of mortality for the population dynamics of the species. The first step in developing the conceptual models was to summarize available information on coho and Chinook salmon life histories by life stage, focusing on information from the Study Area. In particular, information on life stage-specific habitat use, growth, and density-independent factors (e.g., fecundity, sex ratio, gravel quality) and density-dependent factors (e.g., age 0+ carrying capacity, age 1+ carrying capacity) that may limit the survival of each life stage, was also obtained and reviewed. We developed a conceptual model based on a review of the available information, and local knowledge of the geomorphic, hydrologic, and biological characteristics of the Study Area.

2.2 Quantitative Population Models

Quantitative population models were developed for coho salmon and fall Chinook salmon in the Study Area in spreadsheet form using Microsoft Excel 2003®. The models are meant to provide a framework for investigating the relative influence of survival at each life stage on the salmon's population dynamics. The utility of these models, like all models, is constrained by the quality of the data that is used within them, and in some cases models may be best used to identify additional information needs.

The models follow the stock-production approach to population modeling, supported by a large body of literature spanning several decades (e.g., Paulik 1973, Moussalli and Hilborn 1986, Sharma et al. 2005). Stock-production modeling is based on the idea of treating the number of individuals (P) in a cohort at a particular developmental stage, as a function of the number of individuals (S) in that cohort at an earlier developmental stage, in the function:

$$P = f(S)$$

Such a function f is called a stock-production relationship. This approach is useful because the important properties of f can often be deduced from general biological considerations. In particular, the function can often be expressed in terms of parameters r and K, where r represents the effect of births and/or deaths independent of density considerations, and K is an upper limit on the population size. Terms used to describe population models are defined in Appendix A.

2.2.1 Model development

The quantitative models were developed using the stock-production framework. Life stages were selected based on the conceptual model and the nature of available data. Once the life stage structure was determined, the basic model structure was assembled in an Excel spreadsheet. A Visual Basic interface was provided for data entry and parameter changes, and it allowed graphical representation of individual stock-production relationships. The basic life stage structure, the factors selected as parameters, and default values for parameters and stock-production forms were determined from local information and literature values.

2.2.1.1 Model input parameters

Model input parameters were selected by: (1) defining life stages most appropriate for modeling, (2) acquiring data, (3) selecting appropriate stock-production models, and (4) selecting values for *r* and *K*.

Life stages

Life stages for modeling were selected based on the biology of the modeled species (Table 2-1). The models were run based on intervals of time between a stock life stage, and the resulting production into the next life stage, defined here as a life-step (e.g., 0+ juvenile to 1+ smolt) (Table 2-2). The life stages of the model correspond to the beginning of these intervals of development. For coho salmon and Chinook salmon, the model was run to estimate production of adults.

Table 2-1. Life stages modeled for coho salmon and fall Chinook salmon.

Life stage	Size (fork length [FL])	
	mm	in
Coho salmon		
Eggs	NA	NA
Emergent fry	~30	~1.2
Early summer 0+	35–55	1–1.8
Late summer 0+	> 55 with no signs of smolting	> 2.2
Spring 1+ smolts	> 55 with signs of smolting	> 2.2
Adult	> 400	> 15.8
Female spawner	> 400	> 15.8
Fall Chinook salmon		
Eggs	NA	NA
Emergent fry	~35	~1.4
Fry	35–55	1.4–2.2
Juvenile	> 55 with no signs of smolting	> 2.2
Smolt	> 55 with signs of smolting	> 2.2
Adult	> 400	>15.8
Female spawner	> 400	>15.8

Table 2-2. Life-steps modeled for coho salmon and fall Chinook salmon.

Life step	Approximate dates	Approximate time interval
Coho salmon		
Emergent fry to early summer 0+	Mid-March through April	< 1 day
Early summer 0+ to late summer 0+	Mid-March to October	7 months
Late summer 0+ to 1+ smolt	October to May	7 months
1+ smolt to returning adults	All year	1.5 years
Adult to female spawner	December to January	1 month
Female spawner to deposited eggs	December through January	1 month
Deposited eggs to emergent fry	December through April	2 months

Life step	Approximate dates	Approximate time interval
Fall Chinook salmon[1]		
Emergent fry to 0+ smolts	March to June	4 months
0+ smolt to returning adults	All year	2.5 years
Adult to female spawner	November to January	1 month
Female spawner to deposited eggs	November through January	1 month
Deposited eggs to emergent fry	November through April	2 months

[1] Age of returning adults based on majority of fish returning as 3-year olds (Waldvogel 2005).

Input data

Three basic types of data were needed to estimate life stage-specific survival: (1) carrying capacity of habitat for each life stage, (2) density-independent mortality prior to attaining carrying capacity, and (3) density-independent mortality occurring after attaining carrying capacity. Analyses based on local data were used to determine many of the input values (see Section 3 for estimates and rationale). The local data used in the analyses presented in this report were provided by Chris Howard (Mill Creek Fisheries Monitoring Program). Any differences in data values from past released reports are due to improvements and corrections made to the existing dataset by Chris Howard. All selected values and their sources are documented in Appendices B and C.

In this modeling approach, habitat area and fish density inputs are used to explicitly represent carrying capacity (K). In addition, mortality is explicitly represented by input values dependent on the rate of increase of the population (r). Factors such as food supply, growth rates, and competition are implicitly included based on available data used to adjust the mortality values. For example, if food availability was low, lower survival may result, and be reflected in the r value (see "*r* and K values" subsection for more detail).

Stock-production models

Four stock-production models were selected to "step" between selected life stages in the population dynamics models. The Beverton-Holt (1957) and "hockey stick" models (Barrowman and Myers 2000) were typically used for density-dependent interactions (e.g., the life-step from emergent fry to 0+ juvenile when habitat limits the population). The linear model was used to reflect density-independent mortality (e.g., the step from eggs to emergent fry, in which mortality is not affected by density). The redd superimposition model was also used for the step from female spawners to deposited eggs. Each of these models is described below.

The Beverton-Holt model allows production to increase toward a limiting carrying capacity (K) for the production (P) of the stock (S). The Beverton-Holt model was used both in its original form, and in another form of the model (Beverton-Holt 2) when production approached carrying capacity at a faster rate than assumed under the original form of the model. The equations for the Beverton-Holt models are:

Beverton-Holt: $P = r \cdot K \cdot S / (K + r \cdot S)$

Beverton-Holt 2: $P = r \cdot K \cdot S / \left(K^2 + (r \cdot S)^2\right)$,

where for all equations:

P = production,

r = density-independent effects,
K = carrying capacity,
S = stock value

The “hockey stick” model was typically used as an alternative to Beverton-Holt 2; it allows production to approach carrying capacity more rapidly than the Beverton-Holt 2 model. The hockey stick model is a piecewise linear relationship with a slope defined by *r* prior to reaching carrying capacity, reflective of complete density-independence (Barrowman and Myers 2000). Once reaching *K*, however, the slope is zero, reflecting complete density-dependence. This model was used to more clearly identify limiting factors. The equation for the hockey stick model is:

$$P = \min(r \cdot S, K),$$

where “min” takes the minimum of the values in parentheses.

The linear model was used to represent relationships with no obviously relevant density-dependence (such as for deposited eggs to emergent fry), and to reflect density-independent mortality for fish during migration (since habitat is not limiting during migration). The equation for the linear model is:

$$P = r \cdot S .$$

The redd superimposition model was used in the population dynamics model to represent the relationship between spawners and deposited eggs. The step from female bull trout spawners to viable eggs in the model has *r* and *K* values based on the fecundity and total available gravel area divided by average redd size. The equation for the superimposition model is:

$$P = K \cdot \left(1 - e^{-rS/K}\right)$$

Although the user can select any of the four models for any of the life-steps, model selection should consider density-dependence or density-independence. Although density-dependent relationships are assumed to govern the transition from stock to production for many life-steps, the rate at which carrying capacity is reached was not modeled. The hockey stick model gives the simplest and most abrupt change from density-independence to density-dependence, and so has the least complex interpretation of all the models. Given the lack of evidence to the contrary, and due to its ease of interpretation, the hockey stick model was used for analysis. Use of the Beverton-Holt 2 model yields a similar result, but with a more gradual approach to carrying capacity.

r and *K* values

The “*r*” value is the effect of births and/or deaths independent of density considerations, resulting from factors such as fecundity, temperature-related mortality, or dependence of egg survival on spawning gravel quality. Depending on the life stage of interest and the stock-production model selected, the input parameter *r* represents the fraction of adults spawning, fecundity, or a density-independent survival rate.

The *r* values were typically based on estimates of survival from the literature and/or results from the past 10 years of data for Mill Creek. For some of the life-steps, the *r* values were based on the literature, since survival is difficult to estimate without individually tagged animals, and life stages younger than juveniles are typically difficult to tag. If the abundance of a particular life stage (say, juveniles) is well below the carrying capacity in a given system, then an estimate of survival under these conditions could be used to represent density-independent survival. For coho salmon, late summer, overwinter, and marine density-independent survival rates were all estimated, based on dive survey, outmigrant trapping, and redd count data.

Coho overwinter survival rates (from late summer 0+ to spring 1+ smolts) for both the West Branch and East Fork were based on estimates of 0+ from late summer snorkel surveys and estimates of 1+ from spring outmigrant trapping during years when 1+ habitat could not be fully seeded due to low densities of 0+ (i.e., 1995, 1996, 1998, and 2001). It is reasonable under these circumstances to assume that survival rates based on these data are primarily related to density-independent mechanisms.

For the West Branch, late summer survival for coho salmon was estimated based on the number of 0+ juveniles estimated in reaches that were becoming dry at the time of the survey. The estimate of late summer survival was calculated as the proportion of the estimated number of juveniles in these potential “dry” reaches to the estimated total number.

Coho outmigration and marine survival was estimated as the proportion of 1+ smolts returning to Mill Creek as adults approximately 1.5 years later. Chinook outmigration and marine survival was estimated as the proportion of 0+ smolts returning to Mill Creek as 3-year old adults, for the purposes of simplifying interpretation of modeling results. Estimates of smolts based on trapping and estimated adults based on redd counts were used. For Chinook, data on annual proportions of 3-year old returns based on Waldvogel (2005) were used in combination with redd count data to estimate the number of 3-year old fish in each spawning year from 1996 to 2004.

The “*K*” value represents the carrying capacity or population size limit for the life stage of interest. The *K* values were typically based on maximum abundance levels using data from the summer juvenile abundance snorkel surveys or outmigrant trapping.

Coho salmon carrying capacity for 0+ early summer juveniles and 1+ smolts was estimated based on the estimates of 0+ from juvenile abundance snorkel surveys and the estimates of 1+ from outmigrant trapping. We based our estimate of early summer 0+ juvenile carrying capacity on estimated abundance from the snorkel surveys. Although snorkel surveys were conducted from July through October, we assumed that density-independent mortality from early summer 0+ to late summer 0+ occurred after this timeframe. Carrying capacity for 1+ smolts was based on higher estimates of 1+ smolt abundance based on outmigrant trapping.

Carrying capacity for Chinook salmon smolts (>55 mm FL) was estimated based on outmigrant trapping data. No efficiency data were collected for Chinook salmon during the study period, so numbers trapped were used, and a relatively high trap efficiency was assumed. Carrying capacity was determined through graphical inspection of the number of smolts versus the estimated number of emergent fry.

We used the fraction of 0+ fish >55 mm FL to help establish the carrying capacity for 0+ smolts in the population model. Data on individual fish size from water year (WY) 1994, 1997, and 2002 to 2005 were used to estimate time-specific (i.e., for March/April, May, and June/July time periods) fractions of the population that were >55 mm FL. These fractions were then applied to the trap totals from the corresponding time periods to obtain an estimate of the number of 0+ smolts in each time period. Assuming trap efficiencies are high for these smaller fish (as compared to 1+ coho smolts, where trapping efficiencies typically ranged from 25 to 50%), this calculation can be used as a conservative estimate of 0+ outmigrants. It is likely that the estimates of the number of 0+ smolts are slight underestimates, as trapping efficiency is less than 100%.

In addition, we also applied the average location and time-specific proportions of fish >55 mm FL (over WY 1994, 1997, 2002 to 2005) to all other years of trapping data where possible. This process extended the time series of smolt estimates so as to improve the ability to estimate carrying capacity.

Stock values

The population dynamics models require a stock “starting point” for the life stage considered to be the first step; the population of that life stage must be known or estimated. For coho salmon, the stock of adults was the starting point population estimate. Based on a recent estimate of the number of redds (assuming the number of adults was equivalent to twice the number of redds), 1,522 adults were used as the initial coho salmon population size and 2,048 adults as the initial Chinook population size, as the starting point for model runs. The initial stock size that was entered into the model only reflects the starting point, and does not typically affect the results when the model is run to equilibrium. However, initial stock size may affect the running of the model through a single production cycle, especially if the starting number of adults cannot produce enough eggs to reach the carrying capacity for deposited eggs.

Spawning escapement was estimated using the time series for redd counts, to estimate the number of coho and Chinook salmon spawners. The objective of this analysis was to apportion the number of "unknown" redds, which was substantial in some years, between Chinook and coho salmon, and steelhead. The apportionment is based on the assumption that the distribution of redd construction dates for each year and each species is Gaussian, and that the detection probability for redds was high.

Finite normal mixture methods (McLachlan and Peel 2000) were used to separate the distribution of the redd creation dates for unknown species into Chinook and coho salmon based on all data that could lead to identity of the species most likely to create the redd. A finite normal mixture model with partial classification was fit to the spawner data. Routines were created in S-Plus which use an expectation maximization (EM) algorithm to obtain maximum likelihood estimates for the model parameters (McLachlan and Krishnan 1997).

2.2.2 Model execution

To run the coho salmon or Chinook salmon population dynamics model, required input values are entered at the end of each row of the spreadsheet (by clicking on the grey button). The user enters appropriate values for parameters such as habitat area and density-independent survival, or accepts the given default values. The initial number of adults is entered directly into the spreadsheet (yellow cells). After entering all of the required input values, the model “steps through” the calculations from “stock” to “production” for each life-step (Figures 2, 3). The models can be run for one generation or to equilibrium.

2.2.3 Evaluation of factors affecting populations

The models were used to evaluate the factors affecting populations of both species. Current habitat conditions were considered, as were habitat enhancements, or management options to increase production of coho salmon or Chinook salmon smolts. Key factors were assumed to be those that influenced the equilibrium adult population size or annual production of smolts.

To determine the life stages and parameters that most affect the equilibrium population, a sensitivity analysis was conducted of the parameters and values in the model. The sensitivity analysis was performed by building a spreadsheet macro that calculated the equilibrium population size of adults with the initial parameter values (Appendices B and C), and then by varying the parameter values as follows:

- Decreasing initial value by 50%,
- Decreasing initial value by 25%,
- Increasing initial value by 33%, and
- Increasing initial value by 100%.

For each change in value, the model calculated the equilibrium population size, holding all other values constant. If altering the value for a parameter resulted in a change to the population size, it was considered a sensitive parameter. However, sensitivity analysis does not explore the potential interactions of multiple input values that are simultaneously increased or decreased. Only changes in values greater than 10% were considered sensitive. For sensitive parameters, additional scrutiny was focused on the source of data, and the potential for management to influence those parameters.

2.3 State-Space Population Models

State-space modeling was used to predict adult escapement for WY 2006, and to improve estimates of adult spawners in other water years. State-space models present a framework which can use multiple sources of data (e.g., spawning escapement, smolt outmigration estimates, and 0+ juvenile estimates) to account for error in adult estimates and to reflect interannual relationships in the true abundance levels over time (Newman and Hankin 2004).

State-space models can take advantage of time series data by alternating between a filtering and predicting step for each time interval (e.g., one year), in which all elements of the state process (true numbers of each modeled life stage) can be estimated based on the observation process (this year's data and observations from all previous years of data) and the underlying state model.

Statistical models for the evolution of the state of the system and the process of observation can be expressed in terms of density functions:

$$p(y_t \mid x_t) \qquad \text{(observation)}$$

$$p(x_{t+1} \mid x_t, y^{(t)} \qquad \text{(evolution of state),}$$

where $y^{(t)} = (y_1, ..., y_t)$.

Four life stages were used in our state-space model: spawners, smolts, pre-smolts, and age 2 adults. The underlying assumption of the state process is that the basic structure of the multi-stage stock-production model (hereafter referred to as the "state model") governs the state process. The model was implemented in S-Plus version 6.2 (Copyright © 1988, 2003 Insightful Corp.).

Stochasticity was incorporated into the multi-stage stock-production parameters, winter carrying capacity for the pre-smolt to smolt step. Winter carrying capacity was modeled as a function of peak winter flow based on a relationship that was observed from the data. A linear model was fit to log-transformed annual smolt abundance estimates and peak winter flows, with resulting model coefficients being used to initialize values for the winter carrying capacity~flow submodel within the state model.

An S-Plus function was then constructed to model the observation process. Variation of the estimates of smolt numbers was used to incorporate stochasticity, with sampling of an assumed normal distribution with mean and variance taken directly from the smolt estimates derived from Mill Creek trapping data. The observation process model was used to assign observation probabilities for the smolt estimates in each year, given a state matrix.

The estimation process was based on a Monte-Carlo approach (Manly 1997) and essentially has two major steps: 1) a Bayesian filtering step, and 2) a prediction step. The Bayesian filtering step initially takes a prior distribution (the state matrix) and "filters" it by simulating the observation process (field sampling), given the initial state matrix (i.e., prior). Observations of smolts and spawners from the Mill Creek dataset were input into the model. Probabilities of observing *y* (the Mill Creek data from a given WY) given the state *x* (5,000 sets of simulated true population numbers based on the assumed initial state matrix and the state model) are generated assuming a normal distribution with means and variances from the Mill Creek data (for the smolt data), and a lognormal distribution with means and variances based on the Mill Creek data (for the spawner data).

An initial state matrix, the "prior", was provided in the model, based on the earliest possible estimates (from WY 1994). However, because the estimates are updated based on each year's data, the starting point is not critical to the model's final output and predictions.

Mathematically, input into the filter step is a representation of $x_{t+1} \mid y^{(t)}$ as $\left\{x_t{}^i\right\}_{i=1}^B$, and the output is a representation of $x_{t+1} \mid y^{(t+1)}$ as $\left\{x_t{}^{i*}\right\}_{i=1}^B$, where * denotes the filtered estimates, and B is the number of simulations (i.e., 5,000).

For the prediction step, the output from the filter step (which consists of B different vectors of the state, xt) becomes the input and is a representation of $x_t \mid y^{(t)}$ as $\left\{x_t{}^{i*}\right\}_{i=1}^B$. Prediction then occurs by running the state model on these input vectors, with the output a representation of $x_{t+1} \mid y^{(t)}$ as $\left\{x_{t+1}{}^i\right\}_{i=1}^B$.

Then another filter step occurs for the next time interval, followed by another prediction step. This process is repeated until there is a prediction for one time step (i.e., year) beyond the final year of observation (i.e., data collection).

Because each input/output is actually a distribution of 5,000 values, only the mean, variance, and quantiles (i.e., 2.5 and 97.5 percentiles to represent a 95% confidence interval) were reported for each filtering and prediction step.

The filtering and prediction calculations can be represented mathematically as:

$$p(x_t \mid y^{(t)}) \propto p(y_t \mid x_t)\, p(x_t \mid y^{(t-1)}) \qquad \text{(filtering)}$$

$$p(x_{t+1} \mid y^{(t)}) = \int p(x_{t+1} \mid x_t, y^{(t)})\, p(x_t \mid y^{(t)})\, d\mu(x_t) \quad \text{(prediction)}$$

The filtered estimates represent our best estimates of the state process variables (i.e., true abundance of smolts and spawners), and the final predicted estimate represents the prediction for WY 2006. After a new year of data collection (i.e., for WY 2006), the filtered estimates will be improved further, and a prediction for the following year (i.e., WY 2007) can also be forecasted.

The log-likelihood of the model was maximized based on three fitted parameters: the slope and intercept from the ln(1+ smolts)~ln(winter peak flow) relationship used to define overwinter carrying capacity; and the smolt to adult survival parameter. The fitted model was then used to calculate the filtered and predicted estimates for 1+ smolts and adult spawners for the West Branch Mill Creek.

3 RESULTS

3.1 Conceptual Models

Conceptual models for coho salmon and Chinook salmon were developed based on a review of the available information, and local knowledge of the geomorphic, hydrologic, and biological characteristics of the Study Area.

3.1.1 Coho salmon

Because juvenile coho salmon generally smolt at age 1+ (or sometimes at age 2+, particularly in colder regions or less productive streams where growth rates are reduced) and must spend at least one summer and winter in freshwater prior to outmigrating to the sea, they tend to establish territories[2] in suitable rearing habitat soon after emergence (as opposed to fall Chinook, chum, pink, and sockeye salmon, which only spend a few weeks or months in the rearing stream). Territories are established to ensure access to sufficient food supply, typically within pool habitats. The role of territories in regulating individual growth is an important mechanism for partitioning a finite food resource among juvenile coho salmon. Larger coho salmon smolts (up to a certain size threshold) have a higher probability of returning as adults (Bilton et al. 1982). If territories were not established and defended by individuals, the result would be either mortality due to starvation or a large number of small smolts which would have very poor ocean survival. The size of individual territories may vary from location to location as a function of food availability and temperature, becoming smaller in more productive habitats or colder streams.

Typically, the maximum number of juvenile coho salmon that can be supported by very good summer habitat is small relative to the number of fry that a few successful redds can produce. Because of this, spawning gravel availability and egg mortality (e.g., as a result of poor gravel quality, redd dewatering, fungus infections, redd scour) rarely have an important effect on coho salmon population dynamics. In other words, any density-dependent mortality that might result from redd superimposition and density-independent mortality resulting from redd scour and poor gravel quality (among other factors) are usually irrelevant because, despite these sources of mortality, far more fry are typically produced than can be supported by the available rearing habitat. Typically, the density-dependent mortality or emigration that occurs when juvenile coho salmon establish territories sets the carrying capacity for juvenile rearing and overshadows other sources of mortality affecting eggs and juveniles. Therefore, the availability of suitable juvenile rearing habitat (either in the summer or winter) is the factor that usually governs the number of coho salmon smolts produced from a stream.

During winter, juvenile coho salmon are typically associated with low-velocity habitats. When temperatures drop and base flows rise, juvenile coho make seasonal shifts to off-channel habitats or undergo temporary shifts (i.e., within a season) during winter freshets. This type of winter habitat provides foraging opportunities at base flows and refuge from displacement by high flows. Over-wintering coho salmon, therefore, are often found in slower velocity habitats such as floodplains, sloughs, off-channel water bodies, beaver ponds, and complex in-channel habitats

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[2] We use the term territory and territory size not only in its traditional sense—as a particular defended area—but also in cases where defense of a particular area may not occur but agonistic behavior by dominant individuals (e.g., nips, fin extensions, charges) effectively determine the maximum density of rearing juvenile coho in a pool.

associated with large woody debris jams. We postulate that such habitat conditions were abundant in many streams in northern California and the Pacific Northwest under historical conditions.

Historically, rearing habitat limitations may have frequently been greater in summer months than in winter. Greater summer limitations may have occurred because in winter, territorial behavior largely disappears and food supply and growth are less important than in other seasons, particularly where winter temperatures are very cold. Additionally, winter habitats such as floodplains and off-channel waterbodies, were often more extensive than summer in-channel habitats. If winter habitat was moderately abundant under historical conditions, greater limitations would be expected during the summer when low flows and warmer temperatures would restrict habitat size and territorial behavior would limit the carrying capacity of a stream. However, because of the profound changes that have occurred in streams throughout coastal Northern California and the Pacific Northwest, such as large-scale removal of in-channel wood, channelization of previously complex drainage patterns, and the construction of levees disconnecting floodplains from the channel, the availability of suitable winter habitat has been greatly diminished. While summer habitat conditions have also deteriorated due to land management activities, it is likely that impacts in many watersheds have disproportionately affected winter habitat. Thus, in our conceptual model for coho salmon, we initially assume that winter habitat under current conditions is in shorter supply than summer habitat.

While it is difficult, if not impossible, to assess coho salmon production from a stream without considering winter habitat limitations, it is also difficult, given the current state of knowledge, to predict rearing densities and habitat utilization during winter freshets. The effects of high flow refuge limitations must often be determined indirectly by examining population abundance before and after the winter season or before and after high flow events.

We used existing available information to evaluate this conceptual model. Our primary objective during this evaluation was to assess the importance of summer and winter rearing habitat to coho salmon production. If summer habitat is not limiting and is fully saturated, we would expect summer densities to be similar between years, suggesting pre-summer mortality does not affect population dynamics. If winter habitat is not limiting, we would expect the number of smolts in the spring to be similar to the number of juveniles found in the summer. These hypotheses are evaluated below.

3.1.1.1 Summer habitat and abundance

Contrary to our conceptual model, data presented in Howard and McLeod (2005a) show considerable variation in year-to-year juvenile summer abundance of coho salmon. In both the East Fork and the West Branch, juvenile numbers are highly variable. This led us to explore the following hypotheses:

(1) All mortality during summer is density-independent; there is no density dependent mechanism. (We would expect to see a linear relationship between the numbers of emergent fry and 0+ fish).

(2) There is extremely high mortality of eggs or early emergent fry; therefore it takes massive numbers of emergent fry for the summer rearing habitat to be fully seeded.

(3) The quality of summer abundance data varied from year to year due to poor data collection (e.g., as a result of poorly-trained personnel, inconsistent field methods or statistics).

(4) In some years, but not all, high density-independent mortality of juvenile coho salmon occurs in summer *after* summer densities have been established through territorial/agonistic behavior. If this is true, it most likely would be the result of low flows greatly reducing available habitat area, making juveniles more susceptible to predation.

Density-dependence versus density-independence

Based on a graphical analysis, it appears that there is evidence for density-dependence for the emergent fry to early summer 0+ step in the West Branch, based on 1+ mean smolt size versus 0+ densities in the preceding summer (Figure 4), and the estimated annual number of 0+ juveniles (from juvenile abundance snorkel surveys) versus the estimated number of emergent fry (assuming a constant survival to emergence of 0.5 and fecundity of 2,300 eggs per female) (Figure 5), West Branch Mill Creek, WY 1995 to 2005). We would expect that 1+ mean sizes would generally decrease with increasing 0+ densities and that the number of 0+ would level off at a given number of emergent fry. For the West Branch, there was evidence for a significant negative relationship between mean 1+ size and 0+ densities (r^2=0.56, p=0.01332), based on a linear model applied to log-transformed data (often appropriate for ratio scale data, such as densities).

There was also evidence that the number of 0+ stabilizes at high emergent fry levels (Figures 4 and 5). Even if assumed values of survival to emergence and fecundity are inaccurate, the shape of the curve relating 0+ juvenile to emergent fry abundance will remain the same as long as fecundity and survival to emergence are roughly constant over the study period. The shape of the curve appears to be asymptotic, indicating a density-dependent relationship (Figure 5).

For the East Fork, this analysis was complicated by the lack of data for 0+ juveniles. Consequently, we graphed the mean 1+ smolt size versus the estimated number of emergent fry, our next best information regarding early life stages. This plot, although not as strong as the West Branch, seems to indicate a decreasing trend in size with increasing numbers of emergent fry (Figure 6), although not significantly so (*p*=0.2514, based on linear regression). The graph of estimated annual number of 1+ smolts versus the number of emergent fry may indicate the effect of two separate density-dependent mechanisms, one in summer and one in winter (Figure 7).

Egg and emergent fry mortality

After reviewing the available data, the second hypothesis that there is extremely high mortality of eggs or early emergent fry, seems unlikely for the West Branch, but possible for the East Fork. High egg or early fry mortality would be most likely due to 1) high peak flows that either scour redds or displace fry, and/or 2) fine sediment deposition in redds that entombs alevins or decreases permeability.

In this study, low summer juvenile abundance is not necessarily associated with high instantaneous peak flows occurring within the incubation period during the previous winter/spring. Relatively low numbers of juveniles (typically <5,000 fish) were estimated in 1995, 1998, 1999, 2000 (5,049 fish) and 2001, yet high peak flows (>30,000 cfs in the mainstem Smith River based on the USGS gage at Jedediah Smith) occurred during 4 of the 5 years during January through March. However, there were also larger numbers of juveniles (>5,000 fish) in other years with high instantaneous peak flows (1997, 2002). There have been few reports of other sources of density-independent mortality such as disease or redd dewatering that might also account for high egg or fry mortality for coho salmon.

High peak flows are common in the Smith River watershed following spawning, however we would not expect frequent scour (i.e., several times per year) to a depth that would affect a significant portion of coho salmon redds. Since the survival of eggs depends in part on redd depths exceeding the depth of scour during the incubation period, salmonid species have faced selective pressures to adjust their reproductive behavior to the typical timing and depth of bed scour. The redd depth for a given species would presumably be the result of an evolutionary trade-off between scour mortality and fecundity. Deeper redds result in reduced scour mortality but require energy that might otherwise be used to produce eggs (e.g., at some point the energy required for a female salmon to dig a deeper redd and have a lower probability of having the eggs scoured would be better spent, in terms of the likely number of her progeny that return to spawn again, on producing more eggs). For example, Chinook salmon typically dig the deepest redds and use largest spawning substrate of any of the Pacific salmon because they tend to spawn in mainstem habitats where bed scour is relatively deep. Similarly, over an evolutionary time-scale, we would expect coho salmon to have adjusted their egg burial depths to at least exceed the depth of scour for floods that have a high probability of occurring, such as bankfull discharge (which will occur on average two out of every three years).

Redd entombment (infiltration of fines into redds that impedes the movement of water and alevins within the redd) may also limit the survival-to-emergence of coho salmon. After hatching, alevins remain within the redds for an additional two to three weeks before emerging from the substrate and establishing territories in suitable habitat. The amount of fine sediment in a redd will limit the ability of alevins to emerge from the streambed. There is a greater presence of fine sediments in the East Fork of Mill Creek and the mainstem Mill Creek (based on field reconnaissance), although gravel quality is apparently high in the West Branch of Mill Creek (Anonymous 1977 and Millan 1980, as cited inWaldvogel 2005). In years where the channel was re-routed due to major storm events, there may be sediment movement downstream which could influence survival in the lower reach of the West Branch. However, redd entombment is not likely to be a major factor in the West Branch of Mill Creek, although it could influence survival in the East Fork of Mill Creek.

Alternatively or in addition to redd scour and/or entombment, entrainment of early emergent fry during winter or spring freshets can lead to high mortality prior to the summer rearing period. Although no direct information is available to assess mortality of early emergent fry, changes in land use within the watershed have likely decreased in-channel shelter, which has the potential to increase the incidence of fry entrainment.

Data quality

The third hypothesis, that data quality varied from year to year, also seems unlikely. Fish population monitoring has been conducted by the same personnel and, with a few exceptions to adjust for changing channel conditions, sampling has occurred at the same sites since 1994. A similar level of sampling effort has been performed in surveys from 1995 to present.

Late summer mortality

After reviewing the available literature, the fourth hypothesis, that in some years high mortality occurs in summer, seems highly likely, particularly for the West Branch. Stranding is one potential source of mortality that could vary from summer to summer and that would occur after summer densities had been established through territorial/agonistic behavior. Within the extent of habitat associated with dry channel or subsurface flow in the West Branch, 0+ juvenile densities were significantly higher than for the rest of the stream based on t-tests comparing densities from the wet reach versus dry reach ($p<0.001$ for each year from 1999 to 2005). Although this may be due to other factors, it seems biologically reasonable that the densities may be higher due to fish becoming trapped in shallower habitat. In addition, there has been documented stranding in the West Branch of Mill Creek (Ozaki 2004, unpubl. data), where available habitat was documented as being dewatered, with several thousand salmonid juveniles observed stranded in drying pools.

3.1.1.2 Winter habitat and abundance

Although high egg and/or early fry mortality may result in less than saturated summer habitat, winter carrying capacity may still be exceeded, and may be the more important limiting factor. We assessed the importance of winter habitat and winter carrying capacity by comparing the available data on summer juvenile coho salmon abundance and spring smolt numbers. If density-dependence is the governing mechanism and an overwintering carrying capacity exists, we would expect in years with sufficient numbers of spawners and typical survival to emergence rates that the number of smolts produced would be nearly constant.

Data supporting density-dependence

If density-dependence exists from 0+ to 1+, and a carrying capacity exists, then we would expect the number of 1+ smolts to level off once reaching a certain number of 0+ juveniles. A plot of 1+ smolt estimates versus 0+ juvenile coho salmon for the West Branch revealed that there is likely some density-dependent mechanism regulating the production of 1+ smolts (Figure 8). The WY 2001 estimate of 10,821 1+ smolts followed a peak flow of 11,403 cfs, the lowest peak flow of all surveyed years (mean flow of 72,597 cfs, based on WY’s 1996 to 2005), indicating that overwinter carrying capacity is likely strongly influenced by flow.

The abundance of 1+ smolts appears to be related to the peak winter flow level[3], with a rapidly decreasing relationship between peak flow and the number of 1+ smolts produced (Figure 9). Juveniles overwintering in Mill Creek would require sufficient quantity and quality of refuge habitat to survive high peak flows. It appears that at lower flows, the West Branch offers much more overwinter rearing habitat than the East Fork, but that the difference between the two tributaries decreases with higher flows.

For the East Fork, 0+ juvenile data was only available for 3 years where corresponding smolt estimates were available. However, density dependence can be evaluated by graphing a time series of 1+ smolt estimates. Smolt numbers are fairly consistent in the East Fork as well, rarely exceeding 2,000 fish. As was the case for the West Branch, in WY 2001 the abundance of 1+ smolts in the East Branch was exceptionally high (3,200 fish) (Figure 10).

Even though 0+ summer habitat does not appear to be fully seeded, it appears that the number of 0+ is usually sufficient to exceed carrying capacity of the overwintering habitat. The number of 0+ juveniles is typically sufficient to meet the carrying capacity of overwintering habitat.

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[3] We used the mainstem Smith River gage records as a surrogate for discharge in Mill Creek. The USGS monitored streamflow and sediment discharge of Mill Creek from 1974-1981. The Mill Creek stream gauge was located approximately 1 km (0.6 mi) downstream of the East Fork and West Branch confluence (drainage area 74.1 km2). The Mill Creek hydrograph closely mimicked the Smith River, although the Smith River has a higher runoff-per-unit-area than Mill Creek (Madej et al. 1986). Refer to Madej et al. (1986) for flow frequency and flow duration curves for the Mill Creek basin.

3.1.2 Chinook salmon

Of the Pacific salmon species, Chinook salmon probably exhibits the greatest diversity in lie history patterns. Juveniles may enter an estuary immediately following emergence or after spending more than a year residing in freshwater (Healey 1991). Thereafter, juvenile Chinook salmon spend from 6 days to 6 months in estuaries prior to moving to the ocean for further growth (Simenstad et al. 1982). Ocean residence may range from 1 to 6 years, and ocean migration patterns are highly variable across populations. Age–at-maturity ranges from age 2 (almost exclusively males) to age 7 (males and females). Adult fish may enter freshwater throughout the year and time of spawning ranges from 1 to 7 months following freshwater entry (Nicholas and Hankin 1988).

Fall Chinook salmon in the Smith River basin appear to be primarily ocean-type fish (defined by Healey 1991), typically migrating to the ocean within 3 months of emergence. We believe that 0+ juveniles may have stayed in larger numbers and reared to larger sizes in tributaries such as Mill Creek than they do currently. Freshwater habitat in the Smith River system is considered relatively pristine, yet there is also a history of logging and effects from logging roads. Currently, forest stands in the Mill Creek watershed lack large conifers necessary for long-term recruitment and retention of instream LWD (Stillwater Sciences 2002), an important component of freshwater habitat. The extent of mainstem rearing may have always supported large numbers of juvenile Chinook in the summer.

The biggest change from historic to current conditions may be in the estuary, where habitat has been much simplified due to agriculture and diking. The majority of Chinook salmon outmigrants appear to arrive in the estuary in early summer and appear to spend only 1-2 weeks here (Zajanc 2003). Consequently, juvenile Chinook salmon outmigrants today may be smolting at smaller sizes than historically, potentially resulting in reduced ocean survival.

3.1.2.1 Spawning habitat

In many systems, spawning habitat is a limiting factor, as fry densities can be relatively high, and spawning gravel is often in short supply. However, for Mill Creek there appears to be abundant spawning gravel based on reconnaissance surveys (Stillwater Sciences, unpubl. data, 2005).

If there is a density-dependent mechanism acting during the step from spawners to deposited eggs, we would expect a limit to the number of emergent fry produced given an increasing number of spawners. Although there is not direct evidence regarding emergent fry, outmigrant trap catch typically consisted of large numbers of smaller fish (<55 mm FL), including emergent fry. As long as density-independent survival of these fish was relatively consistent from year to year, it is reasonable to use these numbers to evaluate the relationship between redds and emergent fry. These numbers are, however, conservative and should be treated as relative measures only, as they are based solely on trap catch and include fish with varying levels of residence time; trap efficiencies clearly less than 100%, with some density-independent mortality likely, which occurs for juveniles between emergence and arrival at the trap (particularly for larger juveniles outmigrating in June/July).

There was evidence of density-dependence once reaching 350 female spawners for the West Branch and about 140 female spawners for the East Fork. For the West Branch, there appeared to be an increasing linear trend until reaching about 350 redds, after which the number of juvenile outmigrants appeared to level off (Figure 11). These data support the idea that density-dependence only occurs at high levels of spawners not typically observed in West Branch Mill

Creek. There appears to be a positive relationship between spawners and juvenile outmigrants with less than 350 spawners, suggesting that there is little superimposition occurring at these levels of escapement.

However for the East Fork, spawning escapement for Chinook has typically exceeded 140 female spawners. It appears that for most years, the abundance of juvenile outmigrants does not exceed 15,000 fish, as compared to 50,000 fish for the West Branch. The years where trap catch exceeded these numbers were low flow years (WY 2001 and 2002), with the two lowest peak winter flows observed during the study period. The difference in the magnitude of juvenile outmigrants between the two branches could be due to density-independent effects, such as survival to emergence, which is likely given that gravel quality appears to be higher in the West Branch than the East Fork (Stillwater Sciences 2005, unpubl. data).

In the East Fork, relatively few female spawners (~140) can produce the typical yearly maximum for juvenile outmigrants (about 15,000 fish). This is supported by the lack of any apparent relationship between spawners and juvenile outmigrants (Figure 11). The relationship in the East Fork contrasts sharply with the positive relationship between the number of spawners and juvenile outmigrants in the West Branch. In the West Branch, the number of juvenile outmigrants appears to increase until about 350 female spawners, with a typical annual maximum of 50,000 juvenile outmigrants. The difference in the relationship between the number of redds and juvenile outmigrant catch seems to suggest that there are different density-dependent mechanisms acting between the two locations.

The density-dependent factors which could be considered at the spawner to emergent fry life-step include redd scour and redd superimposition. Redd scour seems unlikely for either branch, due to the reasons noted for coho salmon (see subsection 3.1.1.1, Egg and emergent fry mortality).

Differences between the East Fork and the West Branch could be due to competition for existing spawning habitat. Early season spawners tend to spawn in the lower East Fork, in contrast to the West Branch, where spawning typically occurs after a high flow event (Figure 12). High flows open access to larger areas of spawning habitat than are available in the East Fork during lower flow conditions. The presence of a positive relationship in the West Branch suggests that the effects of superimposition here are minimal at spawner escapements below 350 female spawners. It seems more likely for superimposition to occur in the East Fork.

3.1.2.2 Juvenile rearing habitat

Even if spawning habitat is being used to its full potential, 0+ spring rearing habitat could be the most important limiting factor if it appears that the number of emergent fry typically produced is enough to exceed the capacity of spring rearing habitat. Based on graphs of 0+ versus emergent fry for the West Branch, it appears that the number of 0+ smolts levels off at high numbers of emergent fry, suggesting density-dependence (Figure 13). Although evidence of such a relationship is less clear for the East Fork, the estimated number of emergent fry are far greater than the number of 0+ smolts produced, suggesting that there are enough emergent fry in most years to fully seed the spring rearing carrying capacity and that there is a density-dependent mechanism operating between emergence and outmigration (Figure 14).

Spring rearing habitat quantity may be dictated by the amount of high flow refuge habitat available for fry or by the typical amount of suitable rearing habitat available in the spring. There was a strong significant relationship between peak winter flow and 0+ smolt estimates (Figure 15), suggesting that entrainment of emergent fry may be the primary density-dependent mechanism. This would help explain the somewhat strong negative relationship between peak winter flow and trapping totals for the West Branch, as trap totals decrease with increasing winter peak flows (Figure 16). This is less convincing for the East Fork, although there is a decreasing trend here as well. It is possible that the effect of fry entrainment may be much greater in the East Fork than the West Branch. The East Fork is more geologically confined and bedrock-influenced than the West Branch, and likely has less velocity refuge than the West Branch (based on Ozaki 2003, unpubl. data).

The two low flow years, WY 2001 and 2002, produced the two highest estimates of 0+ smolts during the study (Figures 13, 14). Low spring base flows may have resulted in abundant low velocity rearing habitat and much higher than typical numbers of 0+ juveniles rearing to smolt size. It is difficult to discern, without early spring or summer dive data, which flow mechanism (i.e., entrainment due to high peak spring/winter flows versus more rearing habitat due to low spring base flows) is more likely to have influenced carrying capacity for 0+ smolts. Regardless, it is apparent that there is a density-dependent force acting on the population from emergence to outmigration.

3.2 Population Models

Population dynamics models were developed and used to help identify critical uncertainties and prioritize restoration actions for coho and Chinook salmon populations. Both models predict adult production by assuming a smolt-to-adult survival rate and running to equilibrium with returning adults. Model input values and their sources, for the coho and Chinook salmon models, respectively, under current conditions, are provided in Appendices B and C.

3.2.1 Coho salmon carrying capacity

A graphical approach was used to estimate carrying capacity for 0+ juveniles and 1+ smolts. The estimation of the value for the model parameter early summer rearing carrying capacity (from the emergent fry to early summer 0+ life stages) was based on the analysis of the relationship between expected numbers of emergent fry and early summer 0+ described in Section 3.1.1.1 (Figures 5). We estimated a 0+ juvenile carrying capacity of 25,000 for the West Branch and 12,000 for the East Fork. The estimated 1+ smolt carrying capacity was 5,500 and 2,300 for the West Branch and East Fork, respectively, based on Figures 8 and 10.

3.2.2 Coho salmon survival

Survival was estimated using data from Mill Creek where possible. Late summer, overwinter, and marine survival rates were all estimated, based on dive survey, outmigrant trapping, and redd count data.

Late summer survival in the West Branch was estimated to be 0.8, assuming 50% mortality of fish in the dry reaches during the summer juvenile abundance snorkel surveys (Table 3-1), based on the estimated number of 0+ juveniles in potential stranding areas. Ozaki (2004, unpubl. data) observed stranding of several thousand salmonid juveniles in the Park reach (approximately 2000 m long) of West Branch Mill Creek during late summer of 2003, confirming the potential for these reaches to strand fish. The extent of stranding may vary annually however, depending on summer base flows and rate of water withdrawal at the Mill Creek campground.

Table 3-1. Potential late summer mortality due to stranding, West Branch of Mill Creek, 1999 to 2006.

Year	Mortality rate (assume 100% mortality of stranded fish)	Mortality rate (assume 50% mortality of stranded fish)
1999	0.30	0.15
2000	0.41	0.21
2001	0.46	0.23
2002	0.26	0.13
2003	0.24	0.12
2004	0.31	0.16
2005	0.16	0.08
Overall	**0.26**	**0.13**

Overwinter survival rate was estimated to be 0.5, based on data from 1995, 1996, 1998, and 2001, years where the number of 0+ juveniles were estimated at near the 1+ smolt winter carrying capacity. However, this rate does not account for any density-dependent mechanisms which are likely still taking place. We used a density-independent survival rate of 0.8 for overwintering, assuming that density-dependent mechanisms were at least partly responsible for the observed survival rates.

Estimated smolt to spawner survival rates ranged from 0.001 to 0.313 (Figure 17), and were highly variable over the course of the study. Survival rates between the East Fork and West Branch appeared to exhibit similar trends. These rates are likely highly influenced by flow and ocean conditions, with flow influencing the timing of outmigration and consequently size of outmigrants (i.e., earlier outmigration resulting in smaller smolts), and likely the survival of these outmigrants in the ocean. The change from a gradual trend to a rapidly increasing trend in smolt-to-adult survival since 2000 was consistent with trends observed for Oregon coastal coho salmon between Cape Blanco and the mouth of the Columbia River (Chilcote et al. 2005).

3.2.3 Chinook salmon carrying capacity

Carrying capacity for 0+ Chinook salmon was estimated based on outmigrant trapping data. No efficiency data were collected for Chinook salmon during the study period, so numbers trapped were used, and a relatively high trap efficiency was assumed. This seems to be a reasonable assumption, given the smaller size of these fish and the greater likelihood of capture, and that the entire stream was funneled into these traps. The carrying capacity for fish >55 mm FL (assumed to be smolts) was estimated at 6,000 for the West Branch and 5,000 for the East Fork, based on graphs of 0+ versus emergent fry (Figures 13, 14). Although there were values greater than these in the dataset, they come from abnormal low flow years (WY 2001 and 2002).

3.2.4 Chinook salmon survival

For Chinook salmon, smolt-to-returning adult ratios ranged from 0.01 to 0.04, based on combined numbers of smolts and adults from the West Branch and East Fork (Figure 18). We assumed that 62% of adults from each year's estimated spawning run were 3-year old fish, based on the ratio of 3-year old returning adults from WY 1993 to 2003 (Waldvogel 2005). These are conservative estimates of survival, as the ratios are based only on the estimated number of 3-year old returning adults. Survival rates from the literature were however comparable. Mean ocean survival rates of CWT release groups from California and coastal Oregon were estimated from 0.07 to 0.16, over the period from 1972 to 1998 (Magnusson 2002).

3.3 Factors Affecting Population Dynamics of Coho Salmon

Following a cohort from the West Branch or East Fork illustrates that although many eggs are deposited, the carrying capacity for eggs is higher than the amount that is currently being deposited. 0+ juveniles in both reaches appear to saturate the available habitat at the current spawner escapement level (based on redd counts from 2005, one female per redd). In the West Branch, there are a sufficient number of 0+ juveniles to saturate overwintering habitat, whereas in the East Fork, overwintering carrying capacity is not currently being reached. Mortality during each life step results in population declines, such that nearly 48,000 emergent fry, 16,000 0+ juveniles, and 8,000 1+ smolts survive to reach the mainstem Mill Creek below the West Branch and East Fork.

Although 1+ smolts are the primary life stage for evaluating the coho salmon population, emergent fry and 0+ juveniles also have considerable ecological value. Coho salmon fry and juveniles may be an important part of the food base for cutthroat trout and possibly juvenile steelhead in the mainstem Mill Creek below the East Fork and West Branch and the mainstem Smith River. Coho salmon that leave the East Fork and West Branch may also rear in the mainstem Mill and/or Smith River and emigrate as 1+ smolts. Emergent fry and 0+ juveniles leaving the Study Area are not necessarily losses, and may potentially survive to become returning adult spawners.

3.3.1 Adult escapement estimates (number of spawners)

Choice of an initial input value for adult escapement does not affect the equilibrium population size or interpretation of the model results. The population model runs were not affected in any meaningful way by the uncertainty associated with the adult escapement estimates. Until summer rearing habitat is fully seeded, the population will continue to increase with each succeeding generation.

3.3.2 Sensitivity analyses

The sensitivity analysis conducted on the coho salmon model under current conditions indicated that the coho salmon population is primarily influenced by the model parameter “1+ smolt ocean survival”, found in the last row of the model. While this parameter strongly affects model results, smolt-to-adult survival estimates have high and currently unquantifiable uncertainty; the smolt survival parameter was only included to allow the population model to estimate escapement and predict equilibrium conditions. However, the influence of this parameter indicates the importance of smolt-to-returning-adult survival in the coho salmon life-cycle. This could have important implications for the Mill Creek coho salmon population as it is not uncommon to have order of magnitude differences in coho salmon ocean survival rates between high and low adult return years (Chilcote et al. 2005).

The model is sensitive (>10% change in spawner abundance) to overwinter carrying capacity, summer rearing habitat carrying capacity and overwinter survival as well as late summer survival (Table 3-2; see Appendix D for more detailed reporting of sensitivity analyses).

Table 3-2. Results of sensitivity analyses for the coho salmon population model.

Parameter	% change (with doubling)	% change (with halving)
1+ smolt ocean survival	77	-42
West Branch overwinter carrying capacity	45	-24
East Fork overwinter carrying capacity	19	-10
West Branch early summer carrying capacity	24	-12
West Branch overwinter survival	6	-12
West Branch late summer survival	6	-12

3.3.2.1 Rearing habitat carrying capacity

Our conceptual model hypothesized that rearing habitat, particularly overwintering habitat, would limit the current population, which is supported by model results. Doubling overwintering habitat in both tributaries increased the adult population size by more than 15% (Table 3-2). Although these values are not to be taken too literally, they do give an indication of the relative magnitude in population change with respect to potential habitat changes. Increasing summer rearing habitat has less of an impact on the population given the current parameter values than increasing overwintering habitat (for the West Branch, only a 24% increase in the adult population size when doubling the habitat, as compared to a 45% increase when doubling overwintering habitat).

3.3.2.2 Survival

Increases or decreases in 1+ smolt ocean survival have a dramatic effect on equilibrium population size, with an increase of 77% with a doubling of ocean survival and a decrease of 42% with a halving of the ocean survival rate. These results highlight the importance of obtaining a 1+ smolt ocean survival estimate as accurate as possible for adult spawner projections to be realistic. In addition, these modeling results indicate that it would be misleading to use trends in adult spawner numbers alone as an indicator of changes to freshwater habitat conditions.

Decreasing overwinter and late summer survival in the West Branch given current conditions has an impact on the population (12% decrease in equilibrium population size), although the change is not dramatic if marine survival is high enough to produce enough returning adults to fully seed the overwintering habitat. Model runs with marine survivals more typical of pre-WY2000 conditions (assumed to be 0.006, based on OPI marine survival indices from Chilcote et al. 2005) indicated that a 50% decrease in any one of the density-independent survival rates would lead to extinction (Appendix D).

3.4 Factors Affecting Population Dynamics of Chinook Salmon

Following a cohort from the West Branch or East Fork illustrates that although many eggs are deposited, the carrying capacity for eggs is higher than the amount that is currently being deposited. Emergent fry in both reaches appear to saturate the available habitat at the current spawner escapement level (based on redd counts from WY 2005, one female per redd). Mortality during each life step results in population declines, such that nearly 125,000 emergent fry and

11,000 0+ smolts survive to reach the mainstem Mill Creek below the West Branch and East Fork.

Although 0+ smolts are the primary life stage for evaluating the Chinook salmon population, emergent fry also have ecological value. Chinook salmon fry may be an important part of the food base for cutthroat trout and possibly juvenile steelhead in the mainstem Mill Creek below the East Fork and West Branch and the mainstem Smith River. Chinook salmon emergent fry that leave the East Fork and West Branch may also rear in the mainstem Mill Creek and/or Smith River and emigrate as 0+ smolts. Therefore, emergent fry leaving the Study Area could potentially survive to become returning adult spawners.

3.4.1 Sensitivity analyses

The sensitivity analysis conducted on the Chinook salmon model under current conditions indicated that the Chinook salmon population is primarily influenced by the model parameter "smolt-to-adult survival", found in the last row of the model. While this parameter strongly affects model results, smolt-to-adult survival estimates have high and currently unquantifiable uncertainty; the smolt survival parameter was only included to allow the population model to estimate escapement and predict equilibrium conditions. However, the influence of this parameter indicates the importance of smolt-to-returning-adult survival in the Chinook salmon life-cycle. This could have important implications for the Mill Creek Chinook salmon population in years with poor ocean conditions and low marine survival rates.

The model is sensitive (>10% change in spawner abundance) to spring rearing carrying capacity, and no other freshwater parameters (Table 3-3; see Appendix E for more detailed reporting of sensitivity analyses).

Table 3-3. Results of sensitivity analyses for the Chinook salmon population model.

Parameter	% change (with doubling)	% change (with halving)
0+ smolt ocean survival	100	-50
West Branch spring carrying capacity	55	-27
East Fork spring carrying capacity	45	-23

3.4.1.1 Rearing habitat carrying capacity

The Chinook salmon conceptual model hypothesized that spring rearing habitat would limit the current population, which is supported by model results. Doubling spring rearing habitat in both tributaries increased the adult population size by more than 40% (Table 3-2). These values provide the relative magnitude in population change with respect to potential habitat changes. Increasing spring rearing habitat in the West Branch has slightly more value (55% increase) than increasing spring rearing habitat in the East Fork (45% increase).

3.4.1.2 Survival

The model is not sensitive to any of the density-independent survival rates in freshwater habitat. It is however very sensitive to survival from smolt to returning adult, with a 100% increase in the number of adult returns by doubling the 0+ smolt ocean survival, and a 50% decrease in the number of returning adults by halving the 0+ smolt ocean survival.

3.5 State-space Model

State-space modeling was used to obtain improved estimates of coho salmon 1+ smolts and spawners (filtered estimates) and predicted numbers of 1+ smolts and spawners, based on the underlying stock-production model and input values for spawner and smolt observations (Table 3-4). Filtered and predicted estimates for 1+ smolts and spawners in the West Branch Mill Creek are presented in Figure 19.

Table 3-4. State-space model input values for coho salmon spawning adults (based on finite normal mixture estimates using redd counts) and 1+ smolts (based on population estimates from outmigrant trapping) in the West Branch Mill Creek.

WY	Spawners	Smolts	
	Estimate	Estimate	Variance
1995	150	2,717	17,823
1996	90	1,277	76,491
1997	104	1,392	108,434
1998	16	5,554	346,580
1999	4	1,342	7,857
2000	4	2,140	39,192
2001	4	10,821	1,345,600
2002	98	5,004	342,225
2003	280	2,931	64,009
2004	76	3,832	219,961
2005	1,120	763	16,384

The 95% confidence intervals for both predicted and filtered estimates typically contained the observed data (Figure 19). Predicted estimates for WY 2006 were 47 spawners (with a 95% CI of 4–194) and 2006 1+ smolts (95% CI of 278–6751).

Predicted values tended to be higher than filtered values for spawners but lower than filtered values for 1+ smolts (Figure 19). Filtered estimates for 1+ smolts were fairly precise, and less precise for spawners. Due to the incorporation of observation data from a given year, filtered estimates are more precise than predicted values.

Filtered and predicted estimates of spawners based on state-space modeling would be more precise if estimates of variance for spawner estimates are obtained. In addition, further improvements to the model could include a predictive equation for smolt to adult survival based on flow and/or ocean conditions. The likelihood of the model could then be maximized based on the choice of a parameter within the predictive equation (e.g., slope or intercept) rather than the current parameter of smolt to adult survival. This would allow for variability in the smolt to adult survival rate over time.

4 RECOMMENDATIONS

4.1 Juvenile/Smolt Monitoring

We recommend a continuation of the existing sampling methodologies of outmigrant trapping and juvenile abundance snorkel surveys. Coho smolt and juvenile data were essential for estimating values for model parameters. We were able to evaluate the potential carrying capacity due to the length of the dataset, and will be able to evaluate any changes in carrying capacity that result from future management actions.

A complete quality control of the juvenile abundance data, similar to that which was conducted for the spawner surveys, is recommended. Once the quality assurance and control is completed, older datasets (WY 1994 to 1998) could be re-run using DARR 2.0 to obtain population estimates for smolts, and more recent years could be re-analyzed for any potential changes.

In the East Fork, estimation of spring and summer rearing habitat carrying capacity was problematic, due to a limited dataset for 0+ juvenile abundance. We strongly recommend continued juvenile abundance snorkel surveys here to better define coho salmon summer carrying capacity, a sensitive model parameter, and improve our understanding of population dynamics in the East Fork. Chinook salmon spring rearing capacity, another sensitive model parameter, may be better defined if these surveys are conducted in the spring, before typical outmigration of any Chinook salmon 0+ smolts. Habitat mapping is recommended to quantify the amount of suitable spring and summer rearing habitat, providing a habitat-based method to assess spring and summer carrying capacity.

Because there is little available data for the mainstem Mill Creek, where there may be substantial rearing of juveniles; we recommend sampling via trapping or snorkel surveys here. The population model could then be expanded to include mainstem Mill Creek parameters as well, improving the capability to assess the Mill Creek coho salmon population.

Trapping data could be used to attempt to separate age classes of steelhead and cutthroat trout in conjunction with evaluating steelhead and cutthroat juvenile densities with regard to coho salmon juvenile densities. This analysis could be focused on effects of interspecies interactions on coho salmon overwinter and summer carrying capacities.

In addition, we recommend winter juvenile abundance snorkel surveys before and after winter freshets to help better quantify overwintering carrying capacity, the most sensitive freshwater model parameter for coho salmon. This monitoring effort could be contextualized within a BACI (before-after control-impact) study design to also help evaluate any habitat enhancement which takes place. Such a study would also help better describe the relationship between flow and overwinter carrying capacity, which in turn would improve the ability of the state-space model to predict adult returns.

4.2 Spawning Surveys

Redd counts were useful in obtaining spawning escapement estimates, and future counts are recommended. The current frequency of redd surveys is adequate for describing spawning timing. The methodology of flagging new redds allowed approximate identification of redd creation dates. These data were critical for assigning a species to redds of unknown species origin.

Minimum escapement estimates involved a fair amount of subjectivity and are not adequate for population monitoring. Estimates of the number of females per redd based on such data are likely to be vast underestimates. Because surveys are conducted on a weekly basis, it is possible for fish to have entered and died between survey dates; therefore, it is not reasonable to assume that carcasses from a current survey were counted as live fish during a past survey. Also, due to the frequency of surveys, it is likely that not all live fish will be counted. Observation probabilities are unknown, hence it is not possible to generate an estimate of the total number of spawners using these data.

More accurate estimates of spawning escapement are needed for the state-space model to better predict adult returns. Weir counts could potentially be used to establish a relationship between the total numbers of spawners and redd counts to improve both past and future estimates for spawning escapement. We recommend that weir counts be conducted for at least 4 to 5 years to establish a relationship between weir-based estimates and redd counts. If a strong relationship exists, we could use redd counts in the future to estimate escapement, with periodic validation from weir counts.

4.3 Restoration Needs

Population modeling identified overwintering habitat as the limiting factor for coho salmon populations, and we recommend that increasing overwintering habitat be the highest priority for any restoration activities. Large woody debris enhancements could potentially help increase overwintering habitat as well as summer rearing habitat. Juvenile coho select habitat primarily on the basis of water velocity (Shirvell 1990), preferring low-velocity habitats throughout the juvenile rearing period. In coastal streams, low-velocity habitat conditions are primarily created by LWD.

The BACI study design recommended in section 4.1 can be used to monitor the response of the coho salmon population to habitat restoration or enhancement. BACI studies have been successfully conducted in other watersheds to evaluate environmental restoration projects, including the response of coho salmon populations to habitat enhancement (Solazzi et al. 2000, Michener 1997).

5 LITERATURE CITED

Albro, P. , and S. Gray. 2002. Juvenile outmigrant monitoring program. 2000 report for the West Branch and East Fork of Mill Creek. Prepared for Stimson Lumber Company, Crescent City, California.

Anonymous. 1997. Stream habitat surveys of tributaries of the Smith River, California. Survey sheets of West Branch Mill Creek. California Department of Fish and Game.

Barrowman, N. J., and R. A. Myers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Canadian Journal of Fisheries and Aquatic Sciences 57: 665-676.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Ministry Agirculture, Fisheries and Food, Fisheries Investigation Series 2, No. 19. London, England.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39: 426-447.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of Fisheries and Aquatic Sciences 52: 1327-1338.

Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models for the dynamics of wild animal populations. Ecological Modelling 171: 157-175.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. U. S. Fish and Wildlife Service Fishery Bulletin 52: 97-110.

CDFG (California Department of Fish and Game). 2004. Recovery strategy for California coho salmon. Species Recovery Strategy 2004-1. Prepared for the California Fish and Game Commission.

Chilcote, M., T. Nickelson, and K. Moore. 2005. Oregon coastal coho assessment. Part 2: viability criteria and status assessment of Oregon coastal coho. Final report Prepared by ODFW, Salem, Oregon.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 55: 2067-2077.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311-393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia.

Howard, C. 2006. Spawning and outmigrant data. Unpublished data.

Howard, C., and R. McLeod. 2005a. Andromous fisheries monitoring of two Smith River tributaries, Del Norte County, California. 1994-2005. Final report. Prepared by Mill Creek Fisheries Monitoring Program, Crescent City, California.

Howard, C., and R. McLeod. 2005b. Chinook and coho salmon adult escapement monitoring for Mill Creek and Rock Creek, Smith River, California. 2003 & 2004 Final report. Prepared by Mill Creek Fisheries Monitoring Program, Crescent City, California.

Madej, M. A., C. O'Sullivan, and N. Varnum. 1986. An evaluation of land use, hydrology, and sediment yield in the Mill Creek watershed, northern California. Redwood National Park research and development technical report Number 17.

Magnusson, A. 2002. Survival rates of coho (*Oncorhynchus kisutch*) and Chinook salmn (*O. tshawytscha*) released from hatcheries on the U. S. and Canadian Pacific coast 1972-1998, with respect to climate and habitat effects. Master's thesis. University of Washington.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods of biology. Texts in statistical science. Second edition edition. Chapman & Hall, London.

McLachlan, G. J., and T. Krishnan. 1997. The EM algorithm and extensions. Wiley Series in probability and statistics. John Wiley & Sons, New York, New York.

McLachlan, G. J., and D. Peel. 2000. Finite mixture models. Wiley Series in probability and statistics. John Wiley & Sons, Inc., New York, New York.

Michener, W. K. 1997. Quantitatively evaluating restoration experiments: research design, statistical analysis, and data management considerations. Restoration Ecology 5: 324-337.

Millan, L. A. 1980. Stream survey for West Branch Mill Creek, Smith River, California. California Department of Fish and Game.

Moussalli, E., and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. Canadian Journal of Fisheries and Aquatic Sciences 43: 135-141.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16: 4-21.

Newman, K. B., and D. G. Hankin. 2004. Statistical procedures for detecting the CVPIA natural Chinook salmon production doubling goal and determining sustainability of production increases. Prepared for CH2M Hill, Corvallis, Oregon.

Nicholas, J. W., and D. G. Hankin. 1998. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Information Reports 88. Oregon Department of Fish and Wildlife, Portland, Oregon.

NMFS (National Marine Fisheries Service). 1997. Endangered and threatened species: threatened status for southern Oregon/northern California coast evolutionarily significant unit (ESU) of coho salmon. Federal Register 62: 24588-24609.

NMFS (National Marine Fisheries Service). 1999. Endangered and Threatened Species: Threatened Status for two Chinook salmon Evolutionarily Significant Units (ESUs) in California; final rule. 50 CFR Part 223. Federal Register 64: 50394-50415.

NMFS (National Marine Fisheries Service). 2005. Endangered and Threatened Species: final listing determinations for 16 ESUs of west coast salmon, and Final 4(d) protective regulations for threatened salmonid ESUs. Federal Register 70: 37160-37204.

Ozaki, V. 2003. Longitudinal profile and pool data analysis. Unpublished data.

Ozaki, V. 2004. Dry reach monitoring West Branch Mill Creek. Unpublished data.

Paulik, G. J. 1973. Studies of the possible form of the stock-recruitment curve. Rapports et Proces-Verbaux des Reunions, Conseil International pour L'Exploration de la Mer 164: 302-315.

Rowdy Creek Hatchery. 1998. Fecundity data. Unpublished data.

Sharma, R., A. B. Cooper, and R. Hilborn. 2005. A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon. Ecological Modelling 183: 231-250.

Shirvell, C. S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47: 852-861.

Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343-364 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, Toronto, Ontario.

Solazzi, M. F., T. E. Nickelson, S. L. Johnson, and J. D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 906-914.

Stillwater Sciences. 2002. Mill Creek property interim management recommendations. Final report. Prepared by Stillwater Sciences, Arcata, California for Save-the-Redwoods League, San Francisco and California Coastal Conservancy, Oakland, California.

Stillwater Sciences. 2005. Field reconnaissance data. Unpublished data.

Waldvogel, J. 2005. Fall Chinook (*Oncorhynchus tshawytscha*) spawning escapement estimate and age composition for a tributary of the Smith River, California: 23 year analysis. Prepared by University of California Cooperative Extension, Crescent City, California.

Zajanc, D. 2003. Residence of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, in the Smith River Estuary, California, 1998-2000. May. Humboldt State University, Arcata, California.

Figures

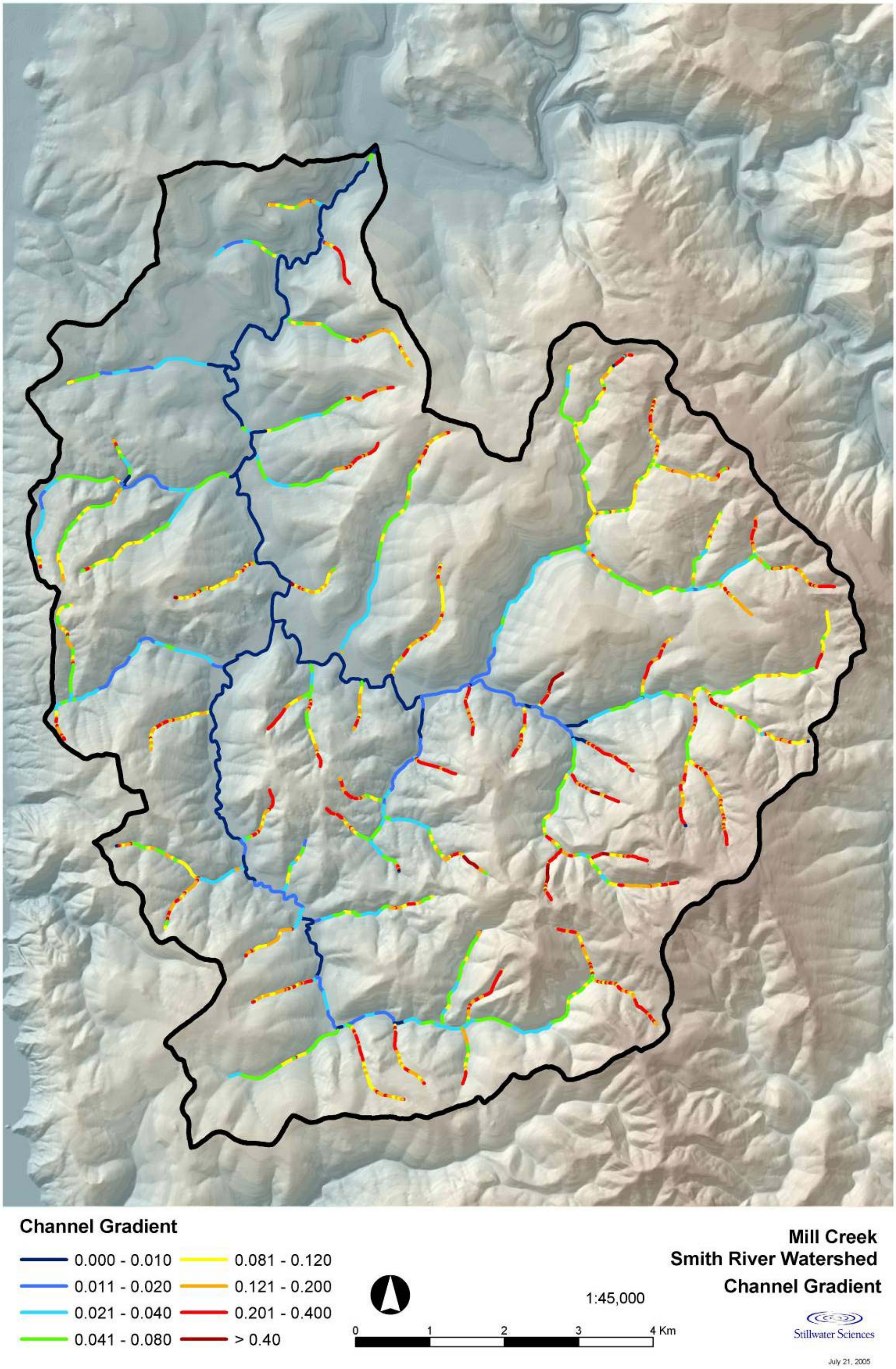
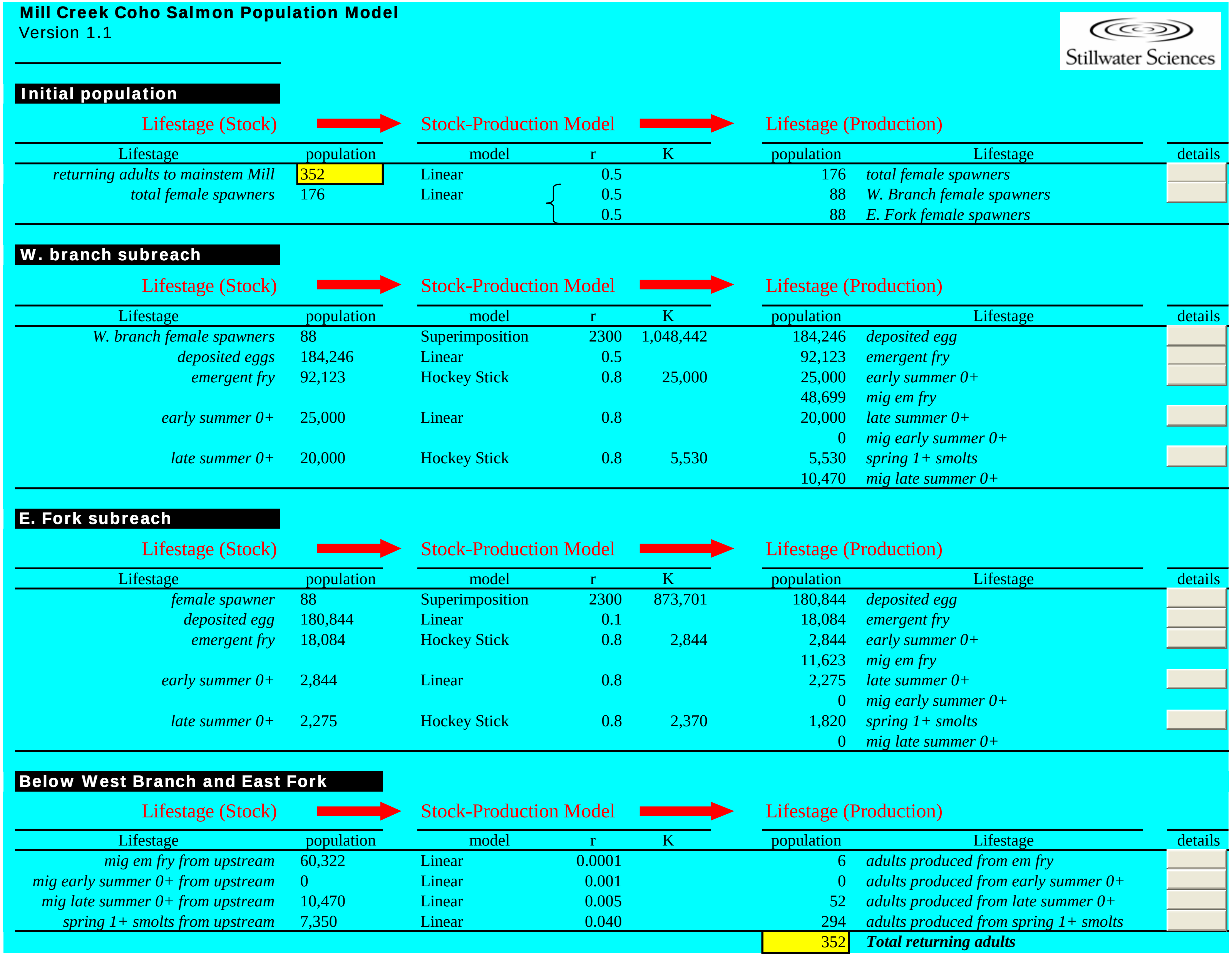


Figure 1. Mill Creek Study Area, Smith River Waterhsed, California.



Mill Creek Coho Salmon Population Model
Version 1.1

Initial population

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
returning adults to mainstem Mill	352	Linear	0.5		176	*total female spawners*	
total female spawners	176	Linear	0.5		88	*W. Branch female spawners*	
			0.5		88	*E. Fork female spawners*	

W. branch subreach

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
W. branch female spawners	88	Superimposition	2300	1,048,442	184,246	*deposited egg*	
deposited eggs	184,246	Linear	0.5		92,123	*emergent fry*	
emergent fry	92,123	Hockey Stick	0.8	25,000	25,000	*early summer 0+*	
					48,699	*mig em fry*	
early summer 0+	25,000	Linear	0.8		20,000	*late summer 0+*	
					0	*mig early summer 0+*	
late summer 0+	20,000	Hockey Stick	0.8	5,530	5,530	*spring 1+ smolts*	
					10,470	*mig late summer 0+*	

E. Fork subreach

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

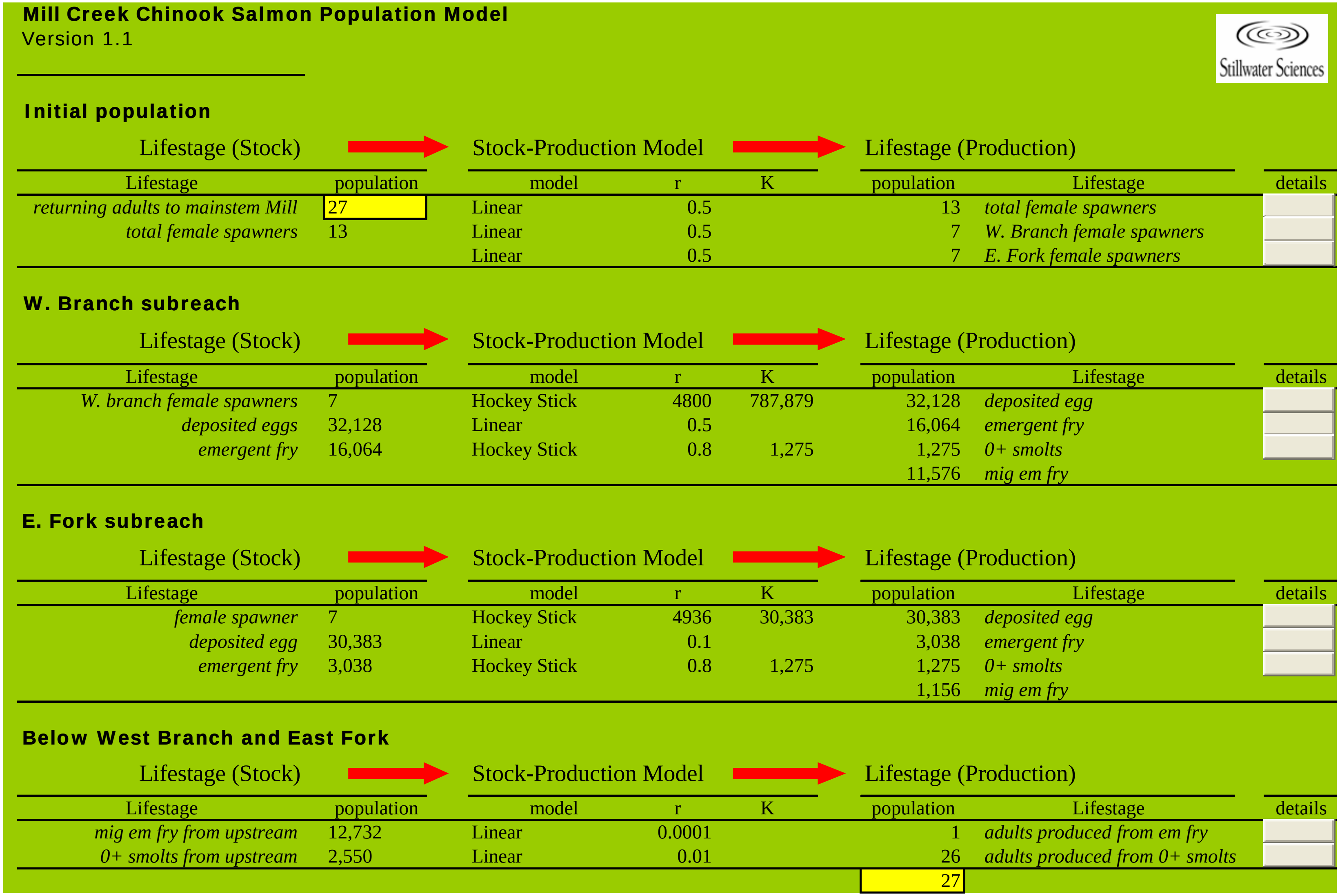
Lifestage	population	model	r	K	population	Lifestage	details
female spawner	88	Superimposition	2300	873,701	180,844	*deposited egg*	
deposited egg	180,844	Linear	0.1		18,084	*emergent fry*	
emergent fry	18,084	Hockey Stick	0.8	2,844	2,844	*early summer 0+*	
					11,623	*mig em fry*	
early summer 0+	2,844	Linear	0.8		2,275	*late summer 0+*	
					0	*mig early summer 0+*	
late summer 0+	2,275	Hockey Stick	0.8	2,370	1,820	*spring 1+ smolts*	
					0	*mig late summer 0+*	

Below West Branch and East Fork

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
mig em fry from upstream	60,322	Linear	0.0001		6	*adults produced from em fry*	
mig early summer 0+ from upstream	0	Linear	0.001		0	*adults produced from early summer 0+*	
mig late summer 0+ from upstream	10,470	Linear	0.005		52	*adults produced from late summer 0+*	
spring 1+ smolts from upstream	7,350	Linear	0.040		294	*adults produced from spring 1+ smolts*	
					352	***Total returning adults***	

Figure 2. Mill Creek Coho Salmon Population Model interface.



Mill Creek Chinook Salmon Population Model
Version 1.1

Initial population

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
returning adults to mainstem Mill	27	Linear	0.5		13	*total female spawners*	
total female spawners	13	Linear	0.5		7	*W. Branch female spawners*	
		Linear	0.5		7	*E. Fork female spawners*	

W. Branch subreach

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
W. branch female spawners	7	Hockey Stick	4800	787,879	32,128	*deposited egg*	
deposited eggs	32,128	Linear	0.5		16,064	*emergent fry*	
emergent fry	16,064	Hockey Stick	0.8	1,275	1,275	*0+ smolts*	
					11,576	*mig em fry*	

E. Fork subreach

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
female spawner	7	Hockey Stick	4936	30,383	30,383	*deposited egg*	
deposited egg	30,383	Linear	0.1		3,038	*emergent fry*	
emergent fry	3,038	Hockey Stick	0.8	1,275	1,275	*0+ smolts*	
					1,156	*mig em fry*	

Below West Branch and East Fork

Lifestage (Stock) → Stock-Production Model → Lifestage (Production)

Lifestage	population	model	r	K	population	Lifestage	details
mig em fry from upstream	12,732	Linear	0.0001		1	*adults produced from em fry*	
0+ smolts from upstream	2,550	Linear	0.01		26	*adults produced from 0+ smolts*	
					27		

Figure 3. Mill Creek Chinook Salmon Population Model interface.

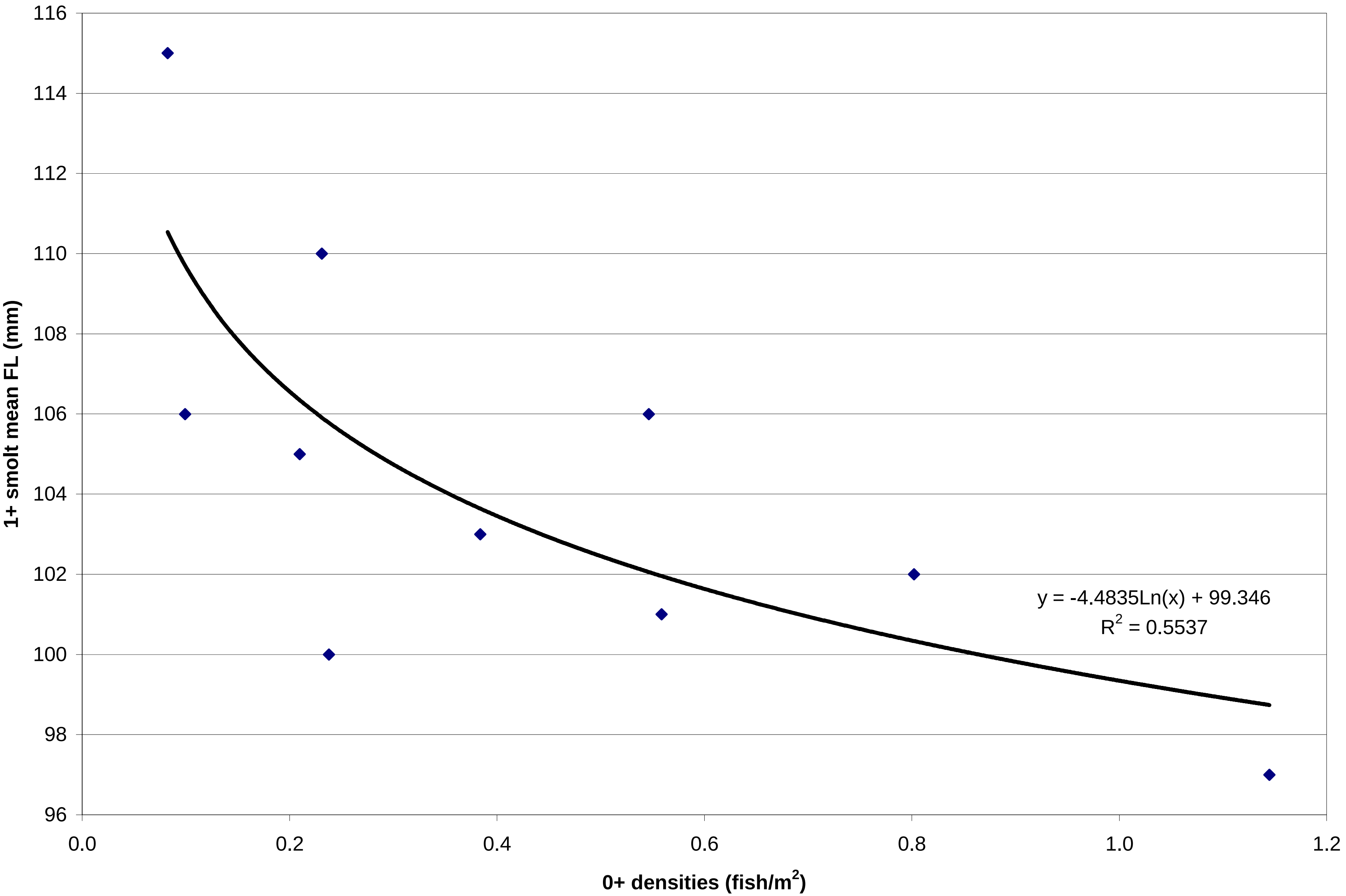


Figure 4. Mean size (fork length in mm) of 1+ coho salmon smolts vs. 0+ densities (fish/m^2) from the preceding water year, West Branch Mill Creek, 0+ densities from WY 1994, 1996 to 2004 and mean smolt sizes from WY 1995, 1997 to 2005.

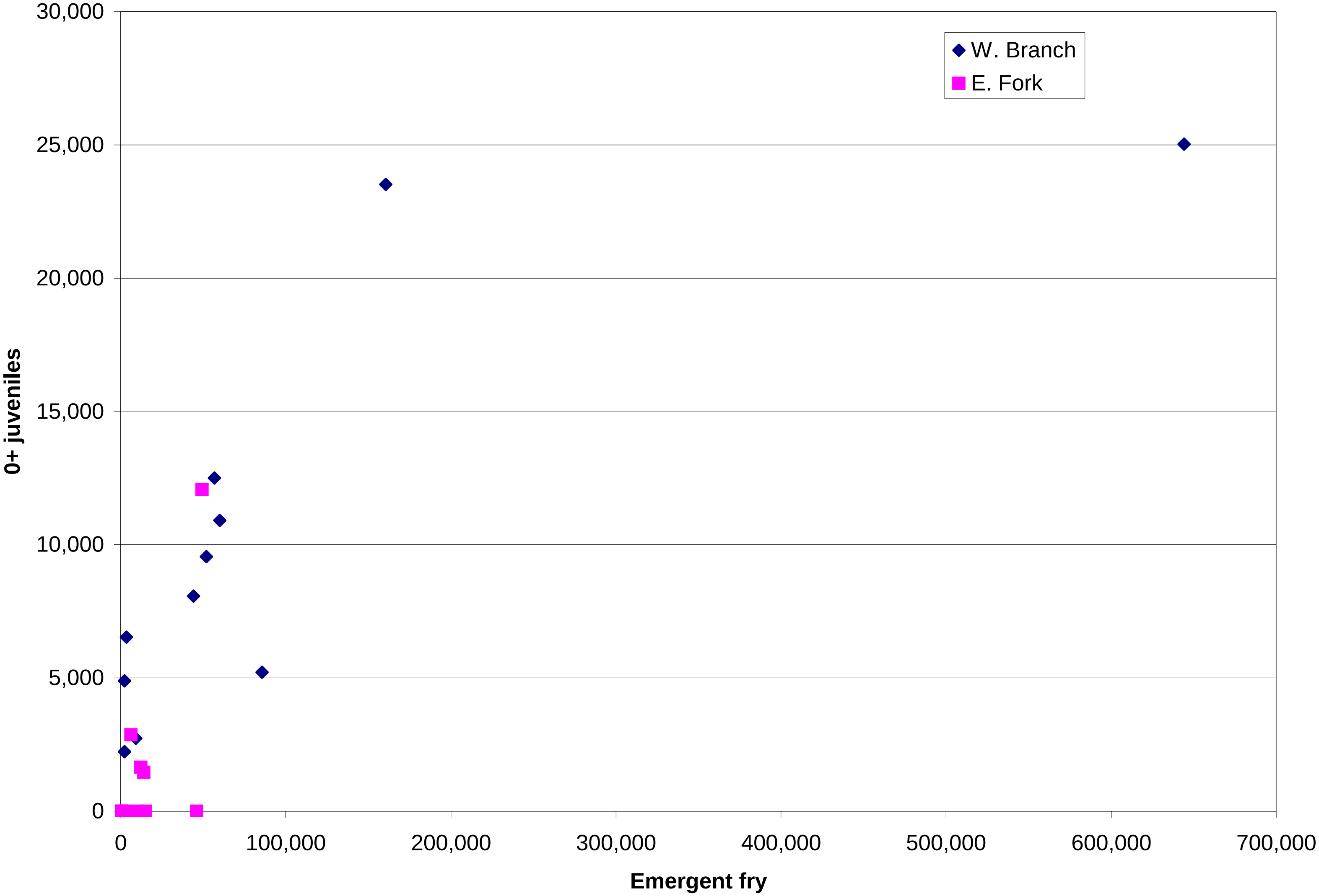


Figure 5. Estimated annual number of coho salmon 0+ juveniles (based on juvenile abundance snorkel surveys) vs. estimated number of emergent fry (assuming a constant survival to emergence of 0.5 and fecundity of 2,300 eggs/female), Mill Creek, WY 1995 to 2005.

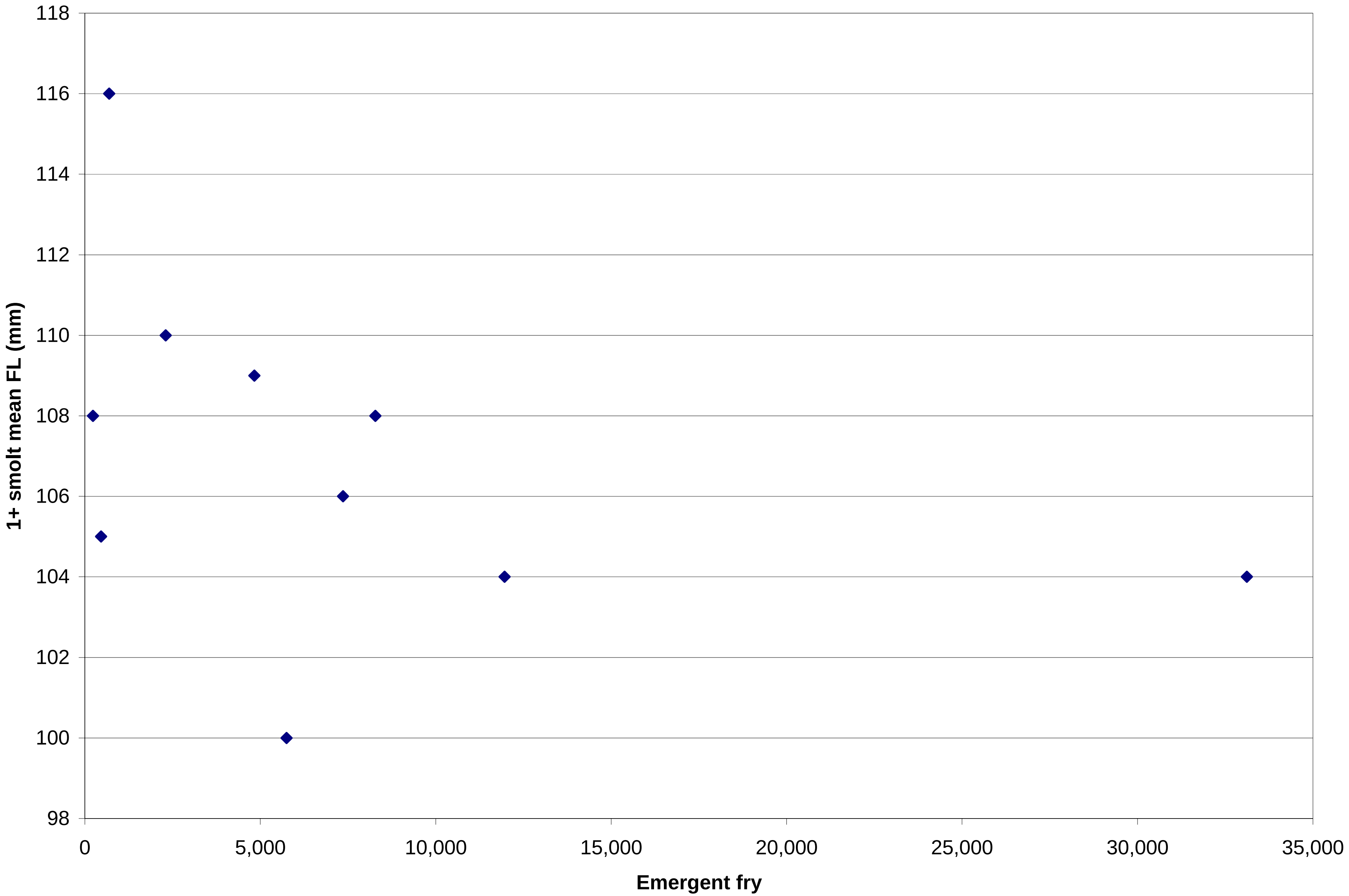


Figure 6. Mean size (fork length in mm) of 1+ coho salmon smolts vs. number of emergent fry from the preceding water year, West Branch Mill Creek, 0+ densities from WY 1995 to 2004 and mean smolt sizes from WY 1996 to 2005.

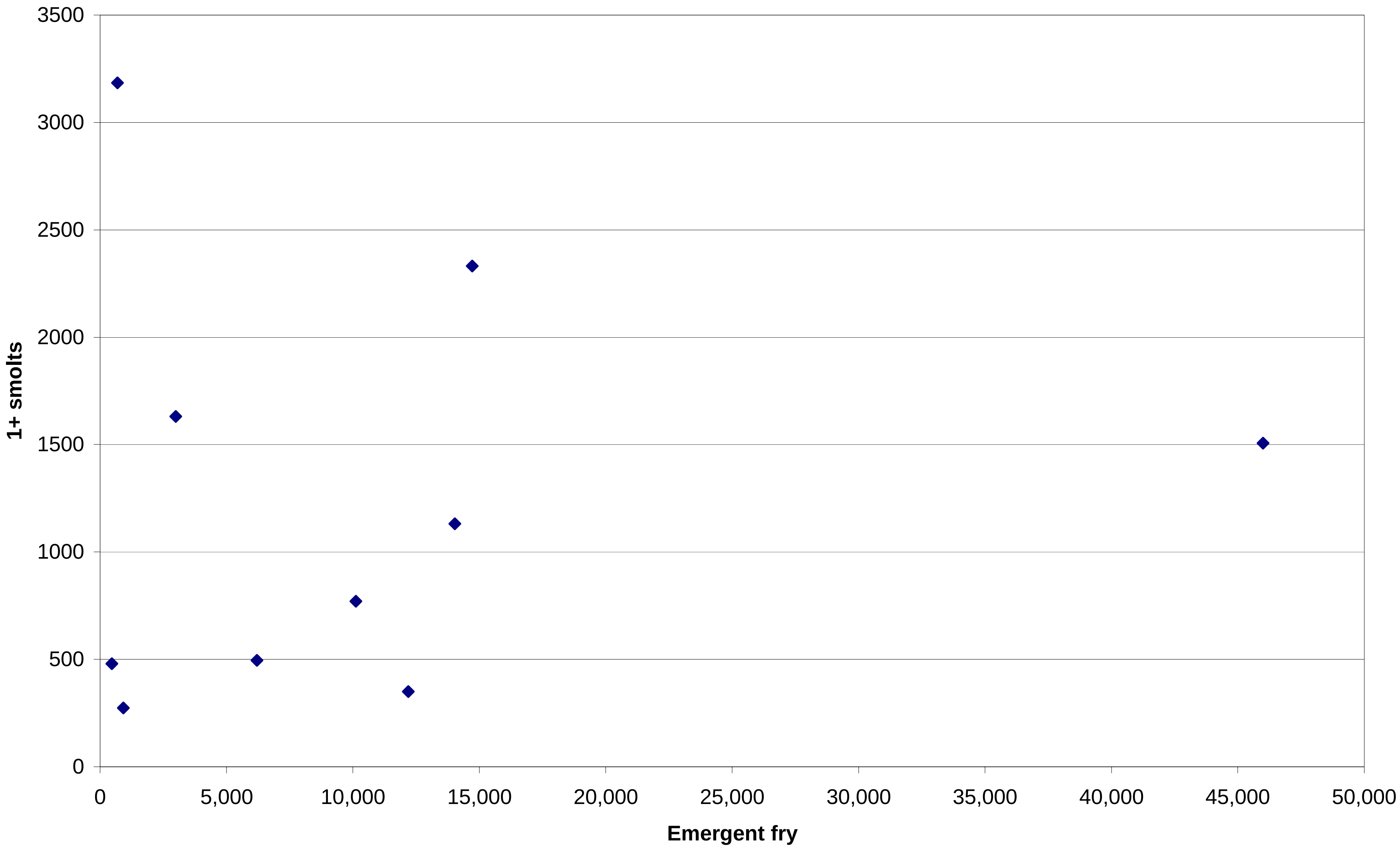


Figure 7. Estimated annual number of coho salmon 1+ smolts (based on outmigrant trapping) vs. estimated number of emergent fry (assuming a constant survival to emergence of 0.1 and fecundity of 2,300 eggs/female), East Fork Mill Creek, WY 1995 to 2005.

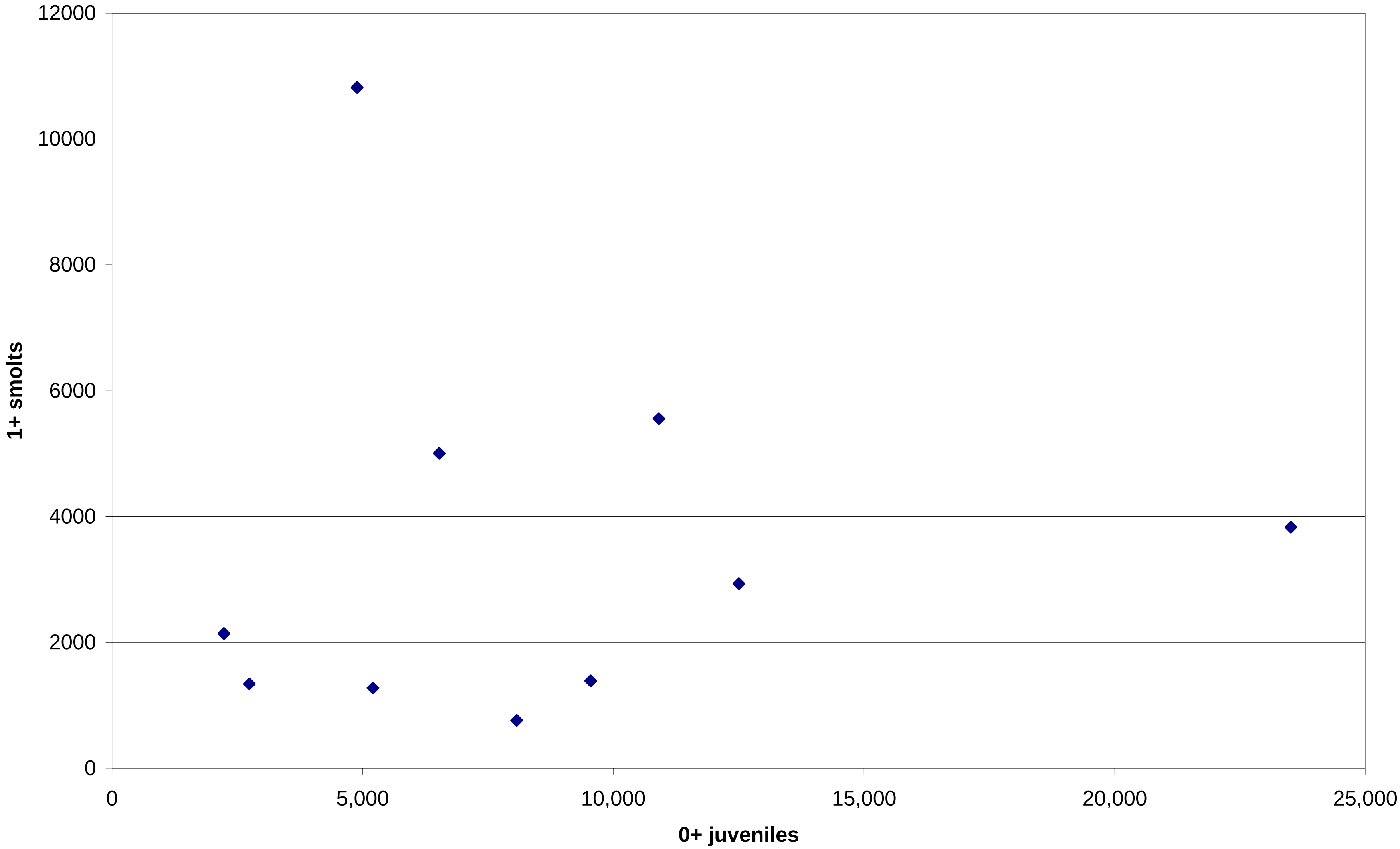


Figure 8. Estimated numbers of 1+ coho salmon smolts versus 0+ juveniles from the preceding water year, West Branch Mill Creek, smolt estimates from WY 1996 to 2005, and 0+ juvenile estimates from WY 1995 to 2004.

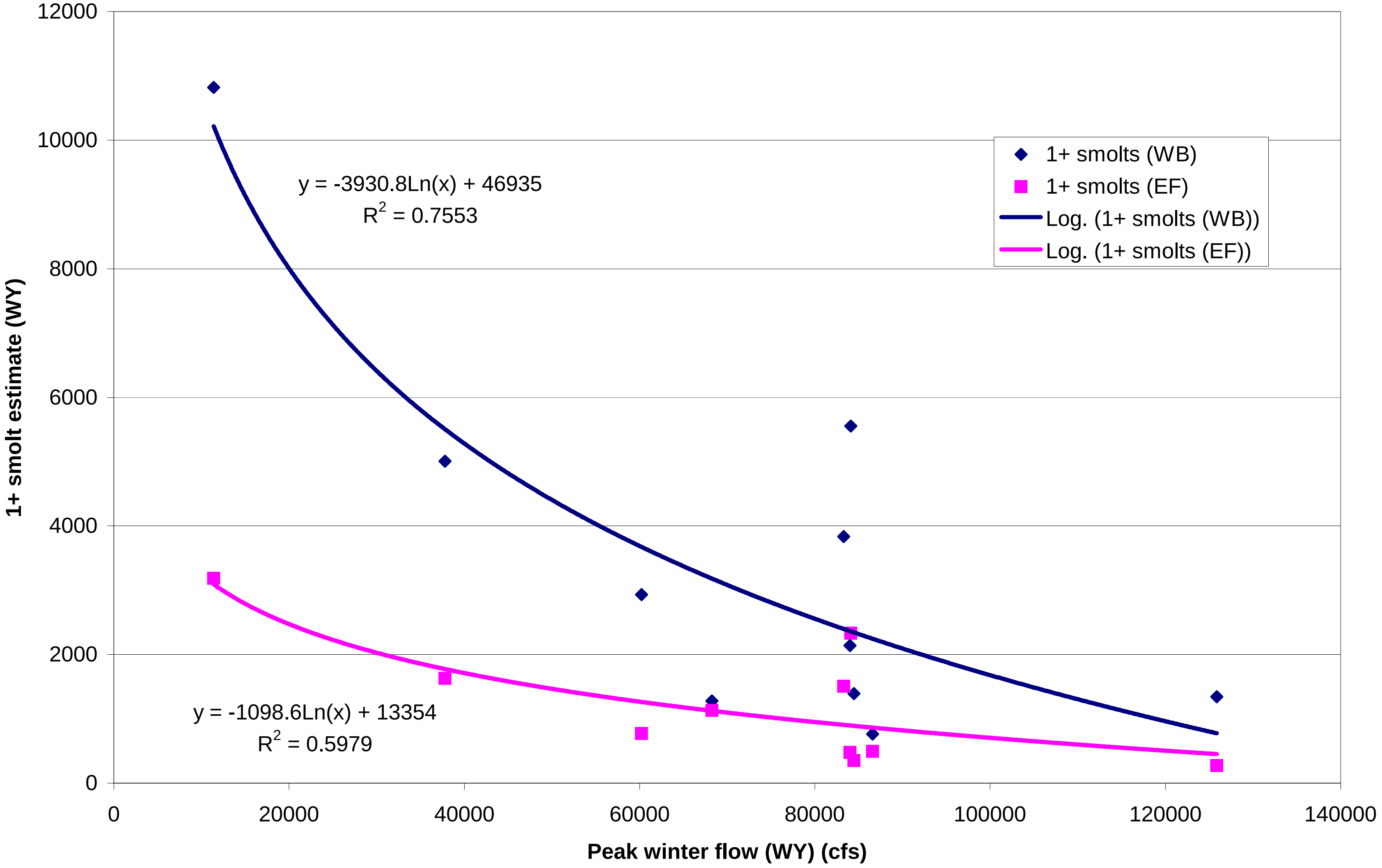


Figure 9. Estimated numbers of 1+ coho salmon smolts versus peak winter flow (cfs) from the preceding water year, West Branch Mill Creek and East Fork Mill Creek, WY 1996 to 2005.

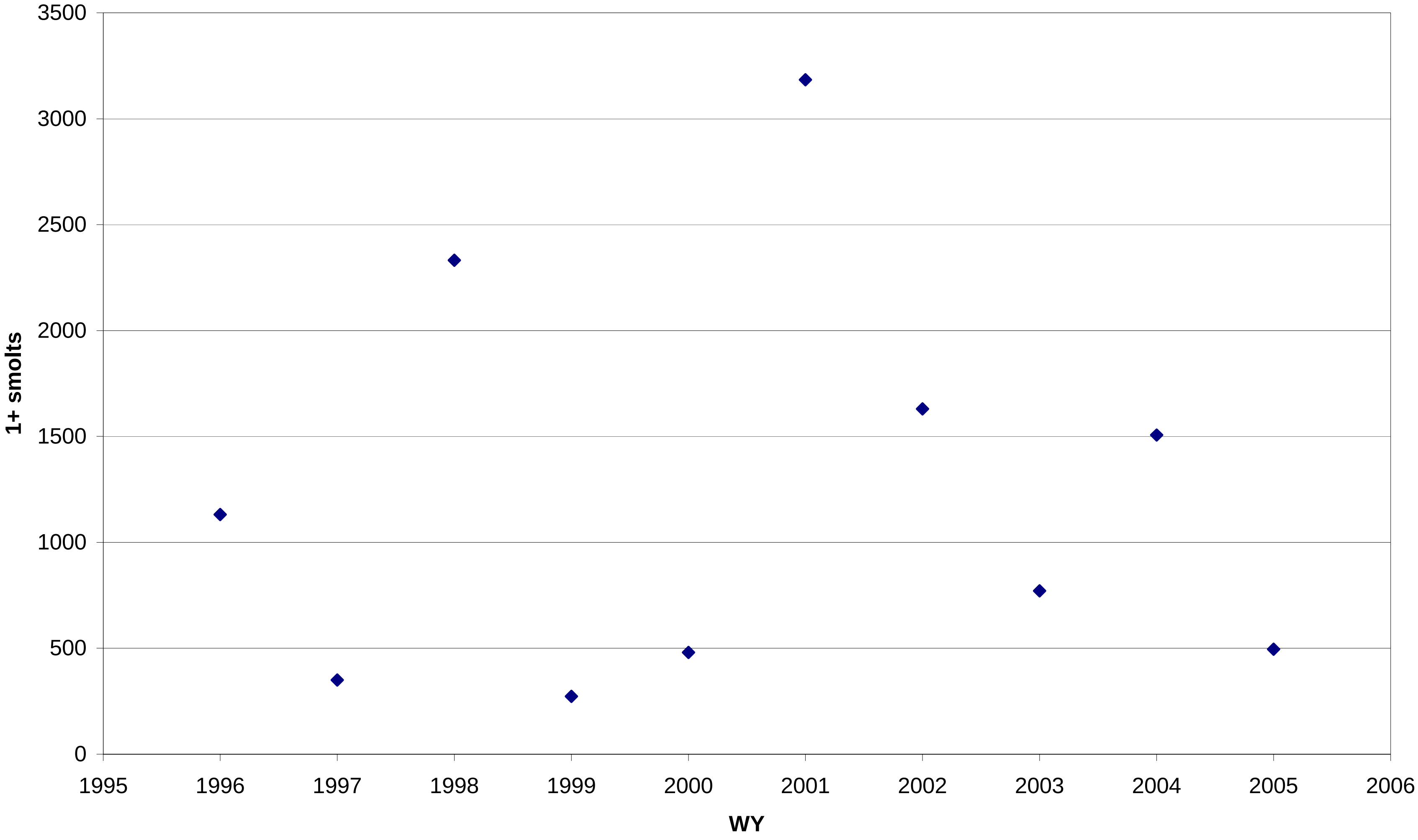


Figure 10. Estimated numbers of coho salmon 1+ smolts versus water year, East Fork Mill Creek.

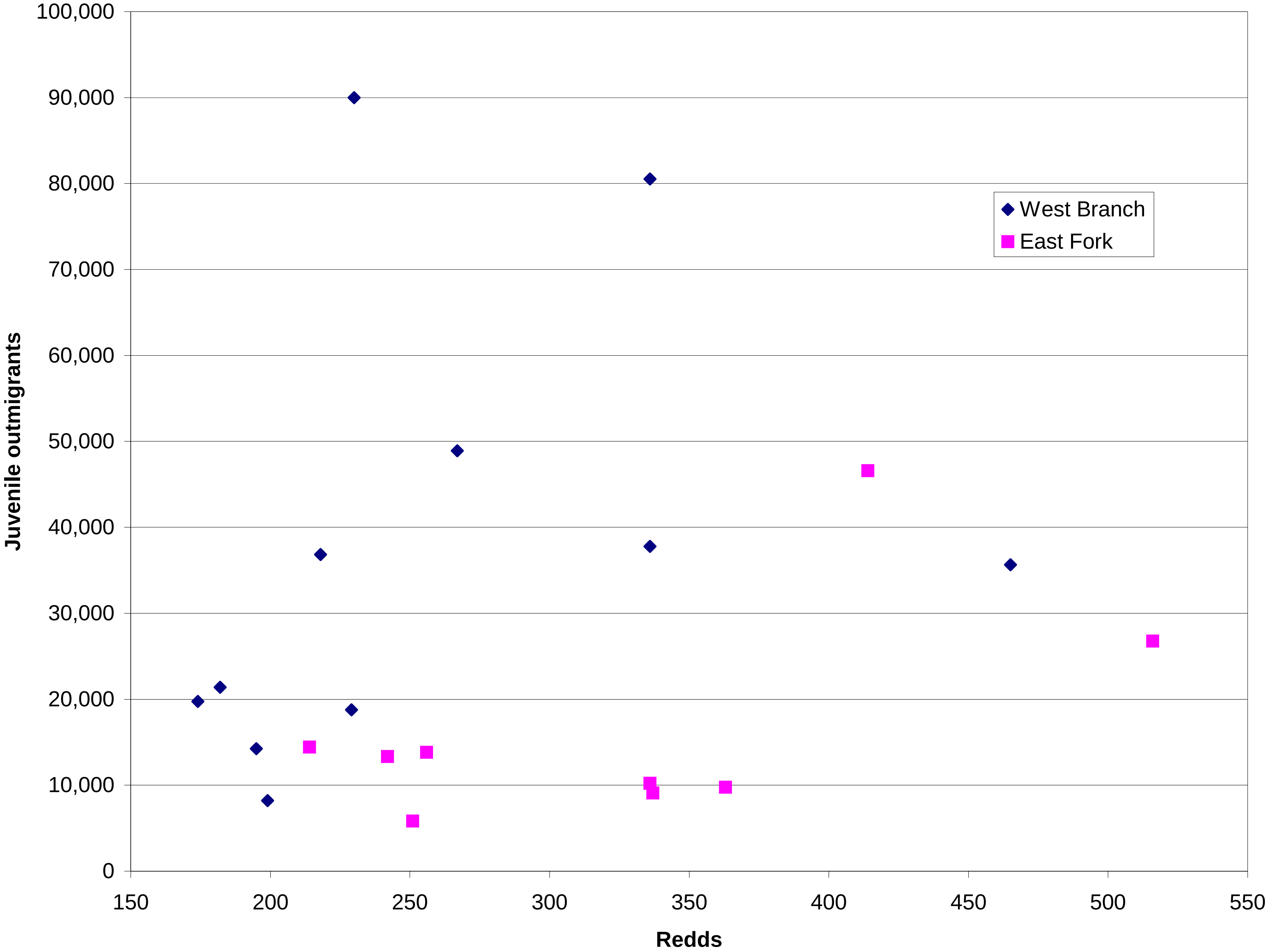


Figure 11. Estimated number of Chinook salmon redds versus number of juvenile outmigrants trapped, East Fork and West Branch Mill Creek, WY 1995 to 2005.

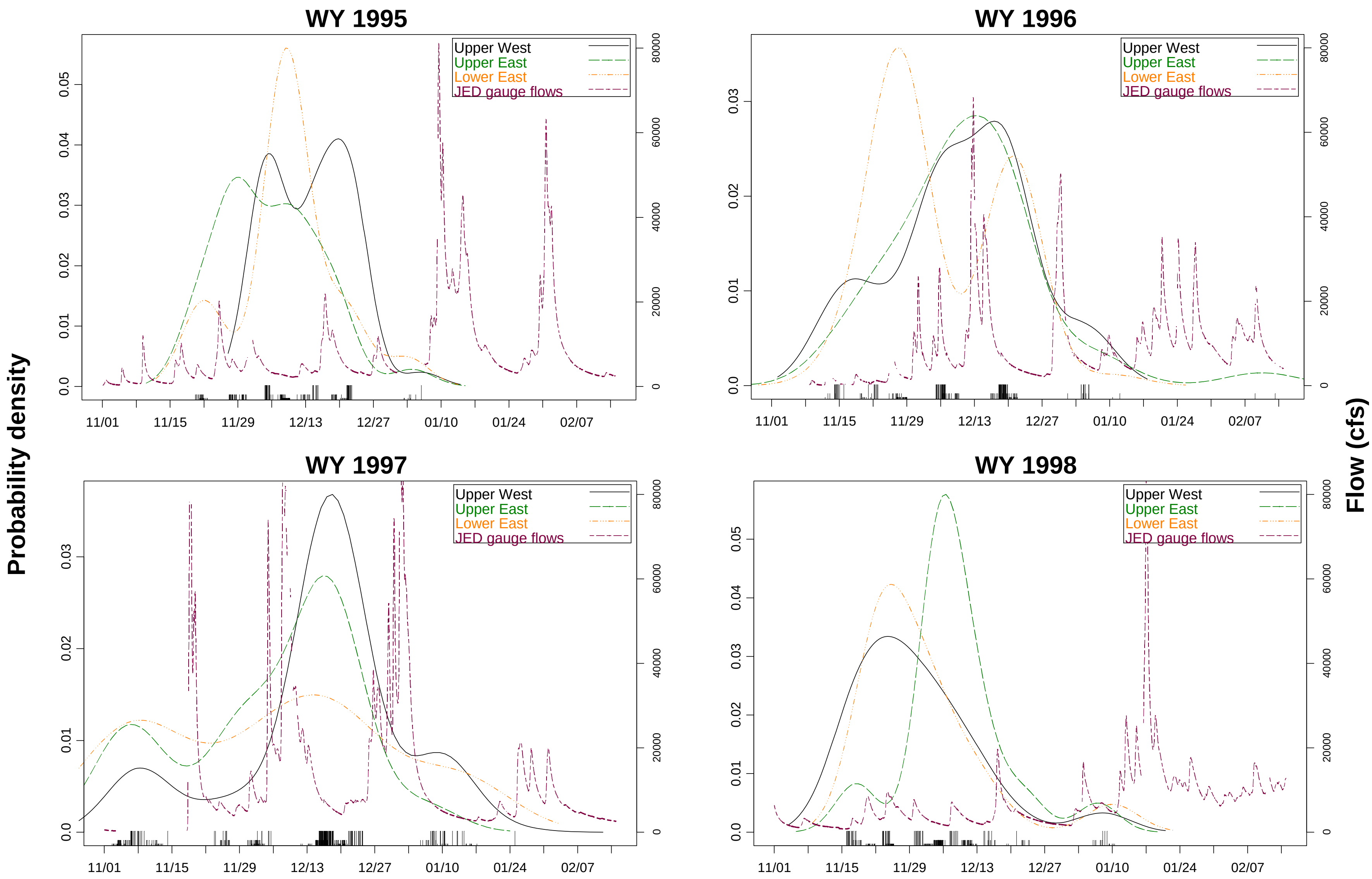


Figure 12a. Spawn timing and flow versus date. Primary y-axis values are probability densities based on smoothing techniques, Bowman and Azzalini (1997).

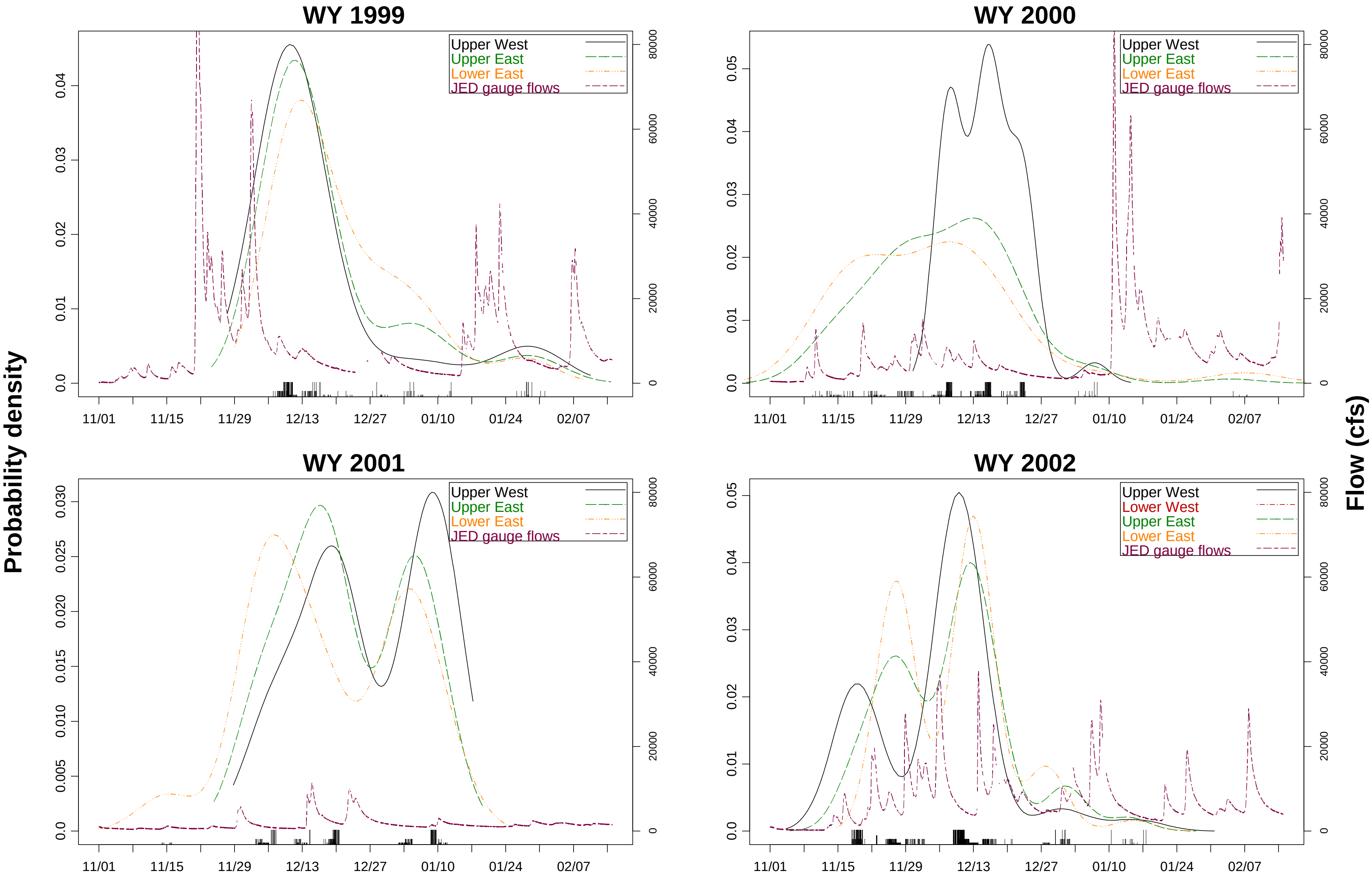


Figure 12b. Spawn timing and flow versus date. Primary y-axis values are probability densities based on smoothing techniques, Bowman and Azzalini (1997).

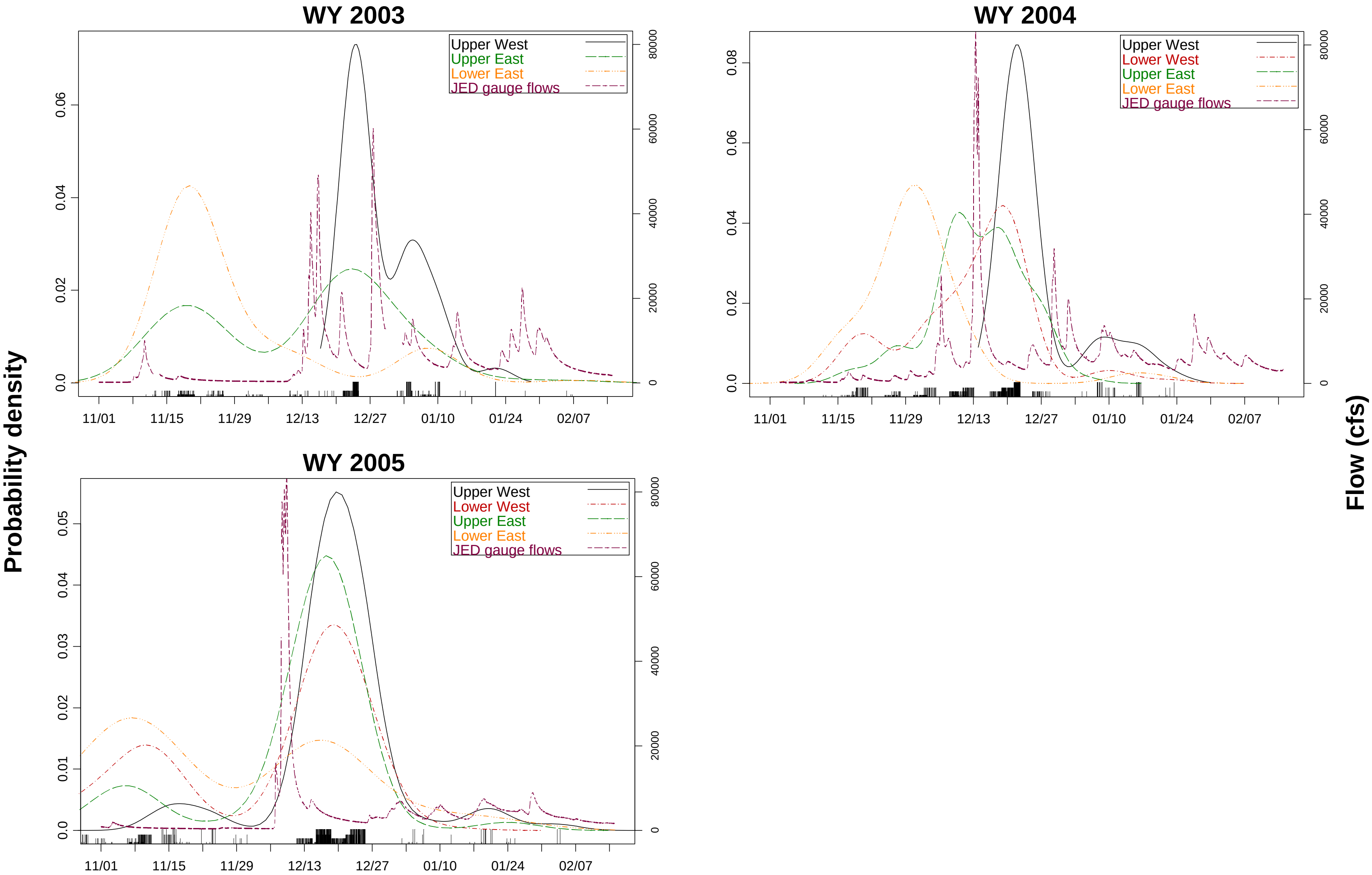


Figure 12c. Spawn timing and flow versus date. Primary y-axis values are probability densities based on smoothing techniques, Bowman and Azzalini (1997).

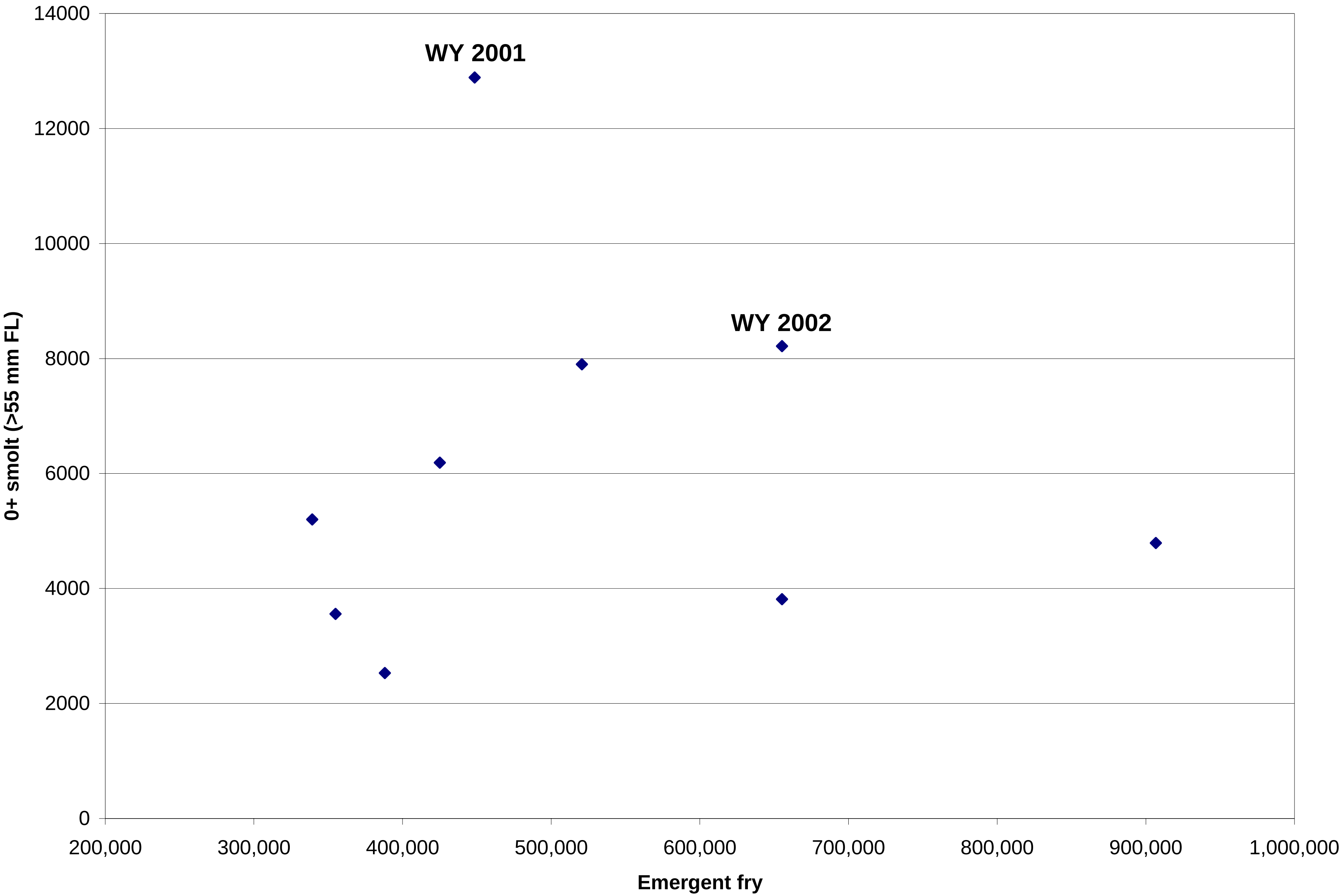


Figure 13. Estimated number of Chinook salmon 0+ smolts (>55 mm FL) based on outmigrant trapping versus estimated number of emergent fry (assuming a constant survival to emergence of 0.5 and fecundity of 3,900 eggs/female), West Branch Mill Creek, WY 1995 to 2005.

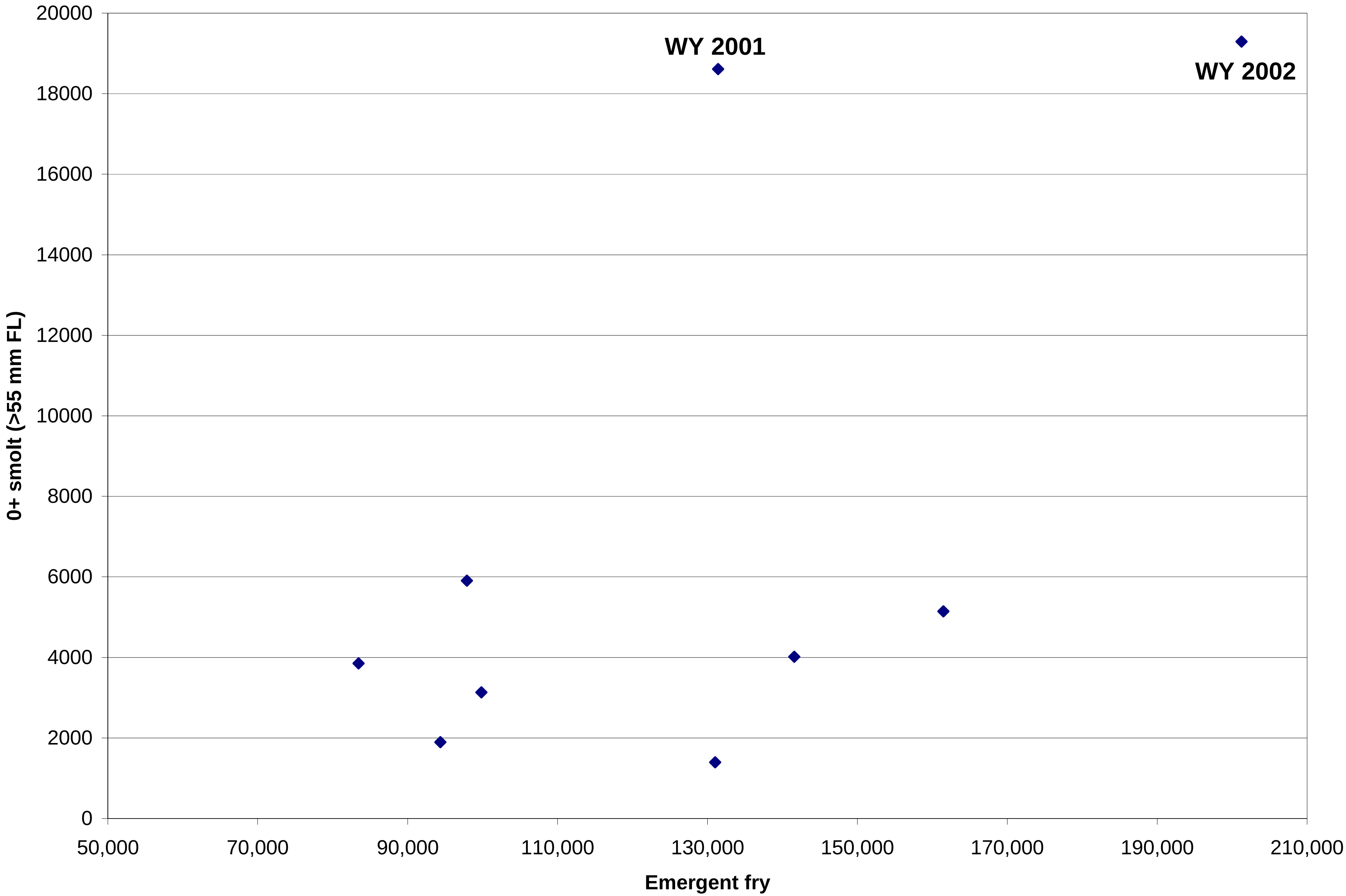


Figure 14. Estimated number of Chinook salmon 0+ smolts (>55 mm FL) based on outmigrant trapping versus estimated number of emergent fry (assuming a constant survival to emergence of 0.1 and fecundity of 3,900 eggs/female), East Fork Mill Creek, WY 1995 to 2005.

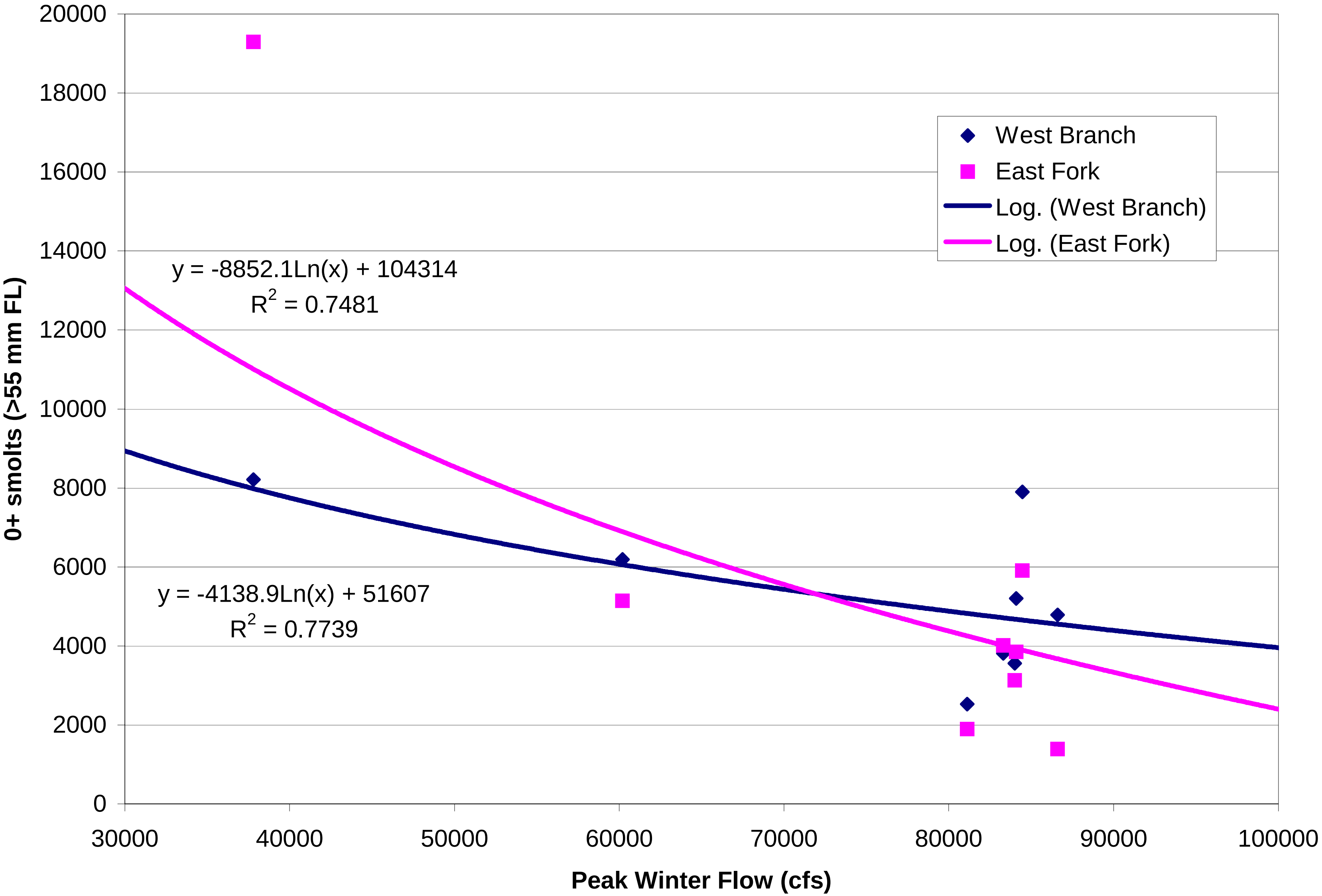


Figure 15. Estimated numbers of Chinook salmon 0+ smolts versus peak winter flow (cfs) from the same water year, West Branch Mill Creek and East Fork Mill Creek, WY 1995 to 2005.

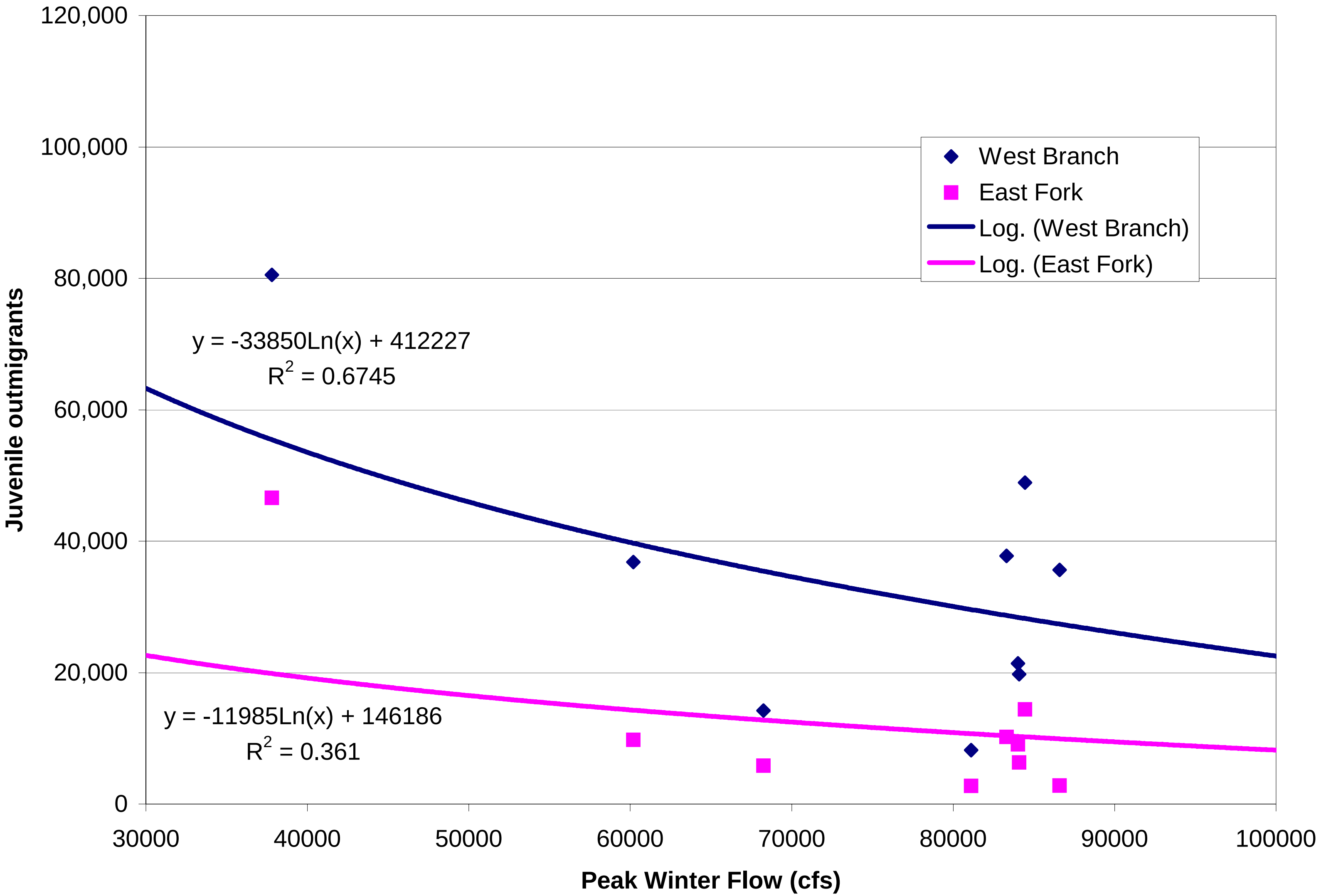


Figure 16. Estimated numbers of Chinook salmon juveniles versus peak winter flow (cfs) from the same water year, West Branch Mill Creek and East Fork Mill Creek, WY 1995 to 2005.

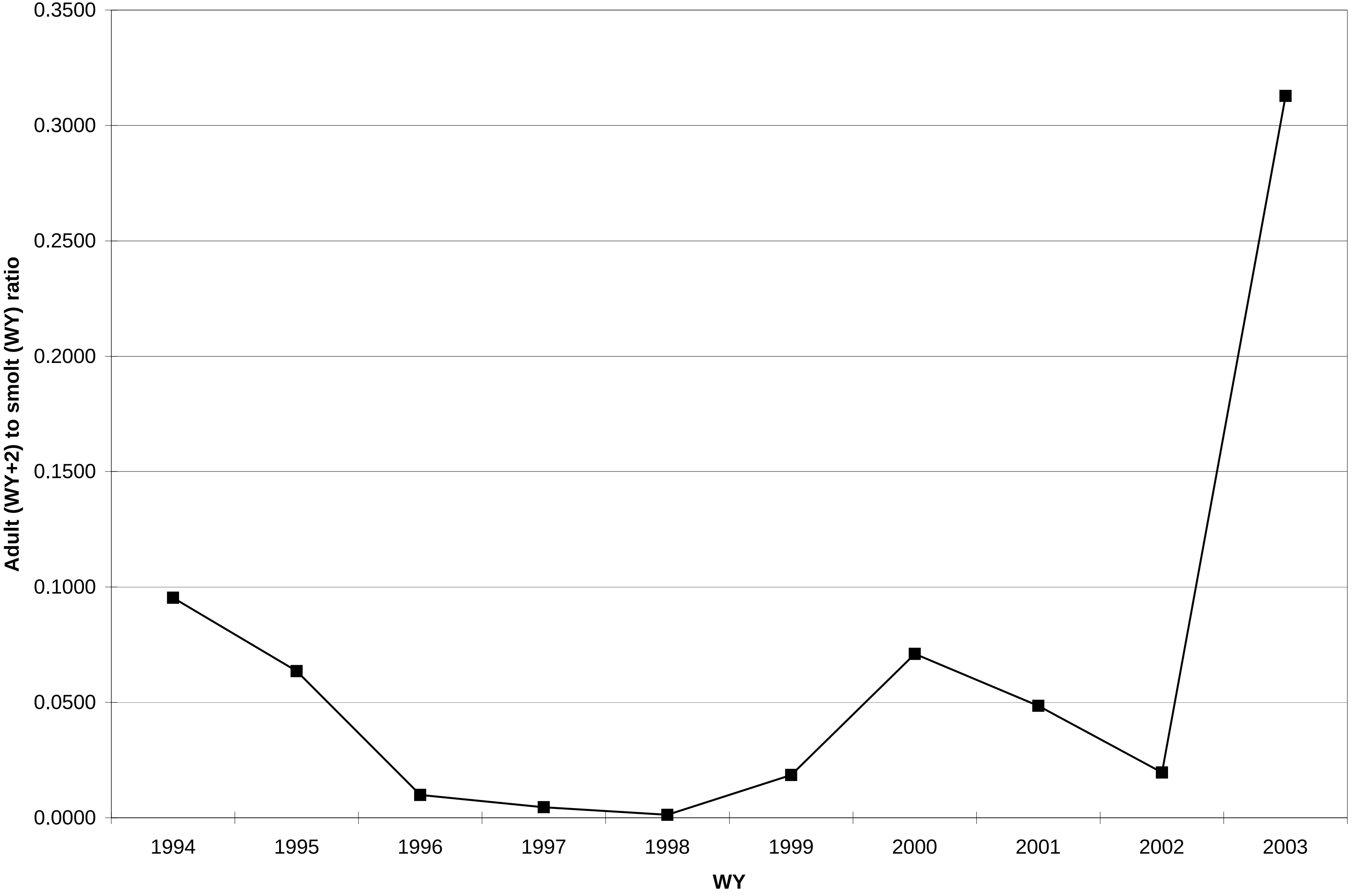


Figure 17. Coho salmon smolt to adult ratios based on smolt estimates from WY 1994 to 2003 and on adult estimates from WY 1996 to 2005 (twice the estimated number of redds), Mill Creek (West Branch and East Fork combined). (Adult estimates from WY 2005 based on raw redd counts rather than estimates.)

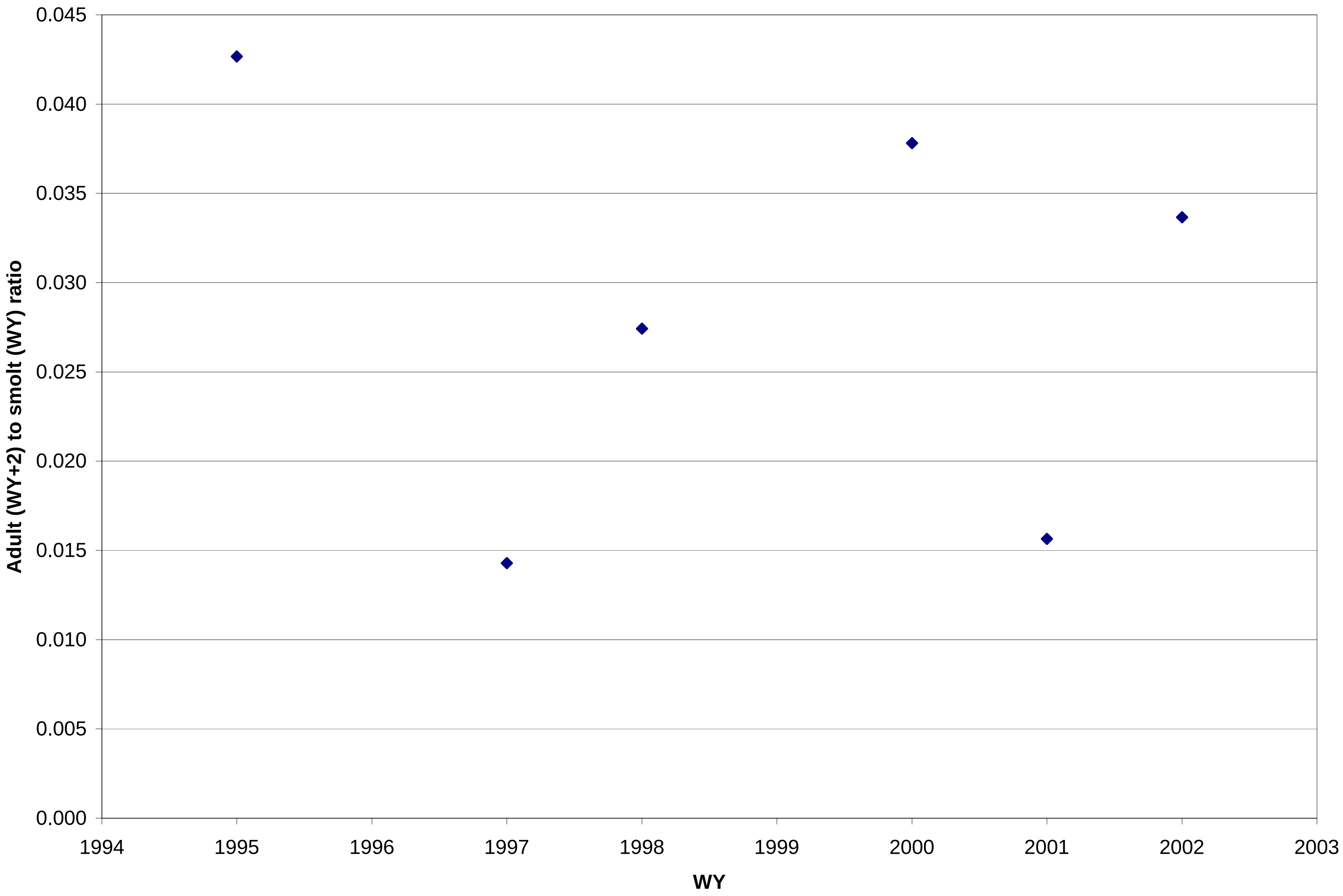


Figure 18. Chinook salmon smolt to adult ratios based on smolt estimates from WY 1995 to 2002 and on 3-year old adult estimates from WY 1998 to 2005 (twice the estimated number of redds produced by 3-year olds), West Branch Mill Creek. (Adult estimates from WY 2005 based on raw redd counts rather than estimates.)

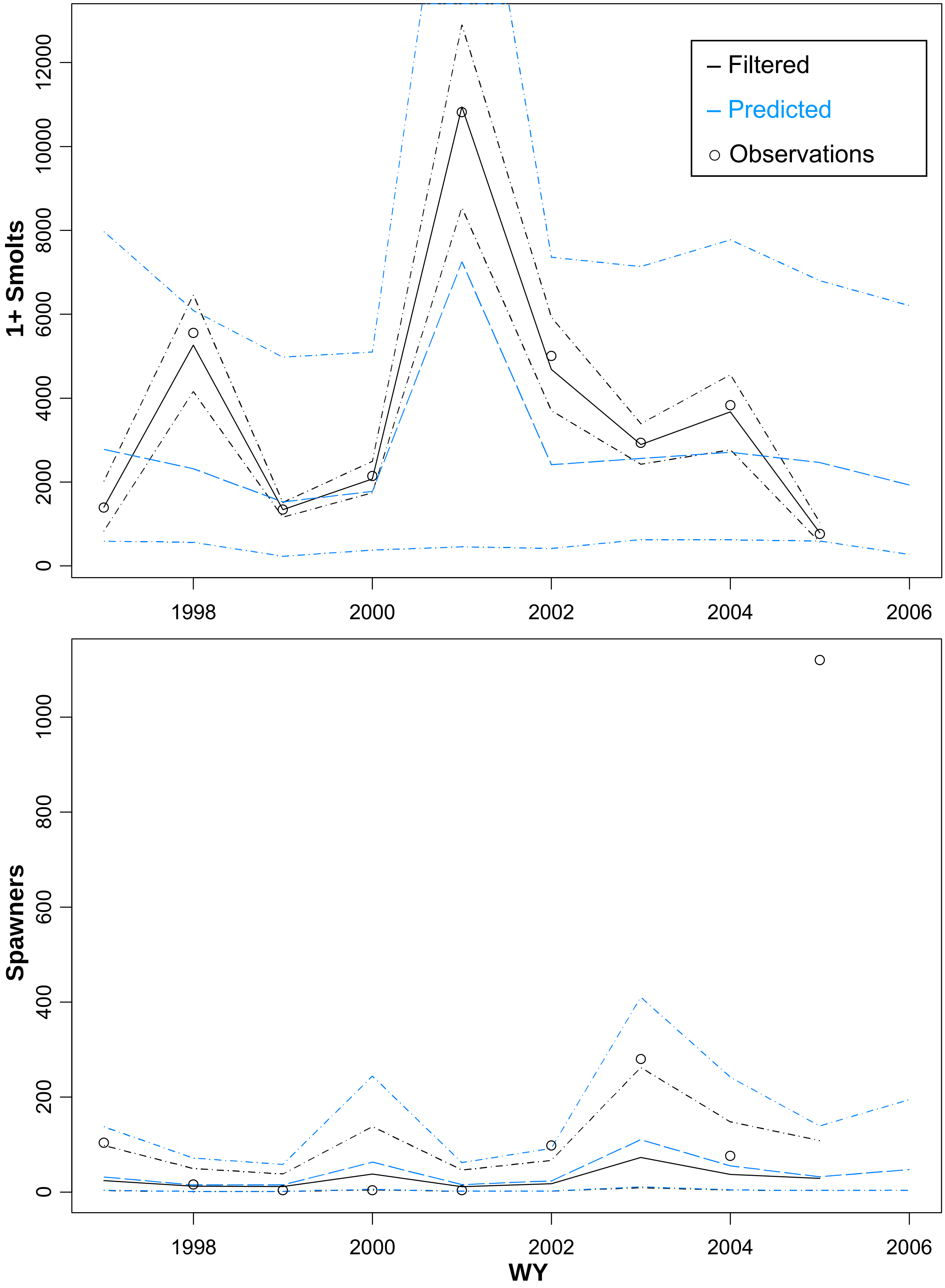


Figure 19. Filtered and predicted estimates of coho salmon 1+ smolts and spawners based on state-space modeling. Solid or long-dashed lines represent point estimates, and short-dashed lines represent 95% confidence intervals.

Appendices

Appendix A

Glossary of terms used for the coho and Chinook salmon population models

Appendix A. Glossary of terms used for the coho and Chinook salmon population models.

Terms	**Definitions**
Beverton-Holt model	Stock-production model that the user may select within the population dynamics models. It is a model commonly used in management of Pacific salmon, based on Beverton and Holt (1957). This model allows production to increase until reaching a certain stock level; above this stock level, production remains constant, at the limit defined by the carrying capacity, K. The population dynamics models allow the user to choose between two versions: Version 1 is the "original" form; Version 2 is a form that allows production to approach carrying capacity at a faster rate (i.e., it allows a steeper curve).
Carrying capacity, K	A density-dependent term used in stock-production models that represents the population size limit for a given life-stage. This term represents density-dependent factors such as spawning gravel area, or abundance of over-wintering refugia.
Cohort	Members of a life-stage that were spawned in the same year.
Density-dependent	Factors affecting the population that are dependent on the population size, such as habitat area.
Density-independent	Factors affecting the population regardless of population size, such as temperature, disease, or stranding.
Hockey stick model	A stock-production model that is a piece-wise linear function with a slope of r for the density-independent phase, and with a slope of zero for the density-dependent phase (once reaching carrying capacity) (Barrowman and Myers 2000).
Rate of population increase, *r*	An input parameter needed in stock-production models. It is a density-independent term that represents the net effect of births and/or deaths, resulting from factors such as fecundity, or dependence of egg survival on spawning gravel quality. Depending on the life-stage of interest and the stock-production model selected, the input parameter *r* represents the fraction of adults spawning, fecundity, or density-independent survival rate.
Linear model	A stock-production model that the user may select within the population dynamics models. This stock-production model assumes a linear relationship between two life-stages, where *r* is the slope of the line.
Life-stage	Temporal stages (or intervals) of a fish's life that have distinct anatomical, physiological, and/or functional characteristics that contribute to potential differences in use of the environment.

Life-step	Interval between a production and stock life-stage (i.e., adult to female spawner)
Production	Output from a stock-production model at a particular life-step.
Stock	Input value required by the stock-production models. It is the first required value entered into the population dynamics model spreadsheets; for example, stock would be the number of fry, for a fry-to-juvenile step.
Stock-production model	Relates the number of individuals P in some cohort at one development stage, as a function (F) of the number of individuals S in that cohort at an earlier development stage: $P = F(S)$. The population dynamics models allow the user to choose from the following four stock-production models: (1) Linear (2) Hockey stick, (3) Beverton-Holt 1 (Beverton and Holt 1957), 4) Beverton-Holt 2, and (5) Superimposition.
Superimposition model	A stock-production model that the user may select within the population dynamics models. The values for this model are based on fecundity, suitable spawning gravel area, and average redd size. This model is used to estimate the number of deposited eggs based on the number of female spawners.

Appendix B

Coho salmon population dynamics model parameters and values under current conditions in the Mill Creek Study Area.

Appendix B. Coho salmon population dynamics model parameters and values under current conditions in the Mill Creek Study Area.

Sub reach	Life-stage	Parameter	Value	Source	Comments
Initial population size	**Returning adults to mainstem Mill Creek as female spawners**	Sex ratio (females to males)	1:1	Howard and McLeod (2005a)	Approximately 1:1 sex ratio based on spawning survey data
		Pre-spawning survival	1.0	Assumption	Assumed pre-spawning survival was typically high
		Proportion of female spawners to the West Branch	0.5	Howard and McLeod (2005a)	Proportion of female spawners default based on spawning survey results; assumes one female per redd.
		Proportion of female spawners to the East Fork	0.5	Howard and McLeod (2005a)	Proportion of female spawners default based on spawning survey results (Howard and McLeod 2005); assumes one female per redd.
West Branch sub reach	**Female spawner to deposited eggs**	Suitable spawning gravel area	3,010 m^2	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on densities of observed spawners and reconnaissance-level mapping of West Branch, 2005 field visit.
		Mean redd area	2.8 m^2	Burner (1951)	Mean redd area based on literature
		Fecundity	2,300	Rowdy Creek Hatchery (1998, unpubl. data)	Assumed fecundity of 2,300 eggs/female based on Rowdy Creek Hatchery data (1993 to 1998)
	Deposited eggs to emergent fry	Survival rate	0.5	Assumption	Assumed to be 0.5, conservative estimate given likely high gravel quality in West Branch (Waldvogel 2005).
	Emergent fry to early summer 0+	Maximum fry density	2.5 fish/m^2	C. Howard (2006, unpublished data)	These data were used to form a product of 25,000 fish, the estimated carrying capacity based on graphical analysis of 0+juveniles versus emergent fry.
		Suitable habitat area	10,000 m^2		
		Density-independent survival rate	0.8	Howard and McLeod (2005b)	Density-independent survival rate assumed high; potential losses due to disease and predation.
	Early summer 0+ fry to late summer 0+	Density-independent survival rate	0.8	C. Howard (2006, unpubl. data)	Density-independent survival rate based on potential losses due to stranding.
	Late summer 0+ to spring 1+ smolts	Maximum juvenile density	0.35	Howard and McLeod (2005b)	Product used to match carrying capacity determined from graphical analysis of 1+ smolts versus 0+ juveniles.
		Suitable habitat area	15,800 m^2		
		Density-independent survival rate	0.8	Assumption	Assumed density-independent survival to be high; majority of winter mortality is likely due to density-dependent effects which happen during peak flow events.
East fork sub reach	**Female spawner to deposited eggs**	Suitable spawning gravel area	3,340 m^2	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on densities of observed spawners and reconnaissance-level mapping of East Fork, 2005 field visit.

Sub reach	Life-stage	Parameter	Value	Source	Comments
		Mean redd area	2.8 m^2	Burner (1951)	Mean redd area based on literature
		Fecundity	2,300	Rowdy Creek Hatchery (1998, unpubl. data)	Assumed fecundity of 2,300 eggs/female based on Rowdy Creek Hatchery data (1993 to 1998)
	Deposited eggs to emergent fry	Survival rate	0.1	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Assumed to be 0.1, estimate based on likely low gravel quality in East Fork, based on ocular estimate from field visit.
	Emergent fry to early summer 0+	Maximum fry density	0.51 fish/m^2	C. Howard (2006, unpubl. data)	Product of density and area to match the estimated carrying capacity from graphical analysis of 0+ versus expected emergent fry.
		Suitable habitat area	23,700 m^2		
		Density-independent survival rate	0.8	Howard and McLeod (2005a, 2005b)	Density-independent survival rate assumed high; potential losses due to disease and predation.
	Early summer 0+ to late summer 0+	Density-independent survival rate	0.9	Assumption	Density-independent survival rate assumed to be high; summer mortality assumed to be low.
	Late summer 0+ to 1+spring smolts	Maximum juvenile density	0.1 fish/m^2	C. Howard (2006, unpubl. data)	Product matches carrying capacity determined from time series of 1+ trapping estimates, highest estimates.
		Suitable habitat area	23,700 m^2		
		Density-independent survival rate	0.8	Assumption	Professional judgment.
Downstream of West Branch and North Fork	**Migrant emergent fry from upstream to adults produced from emergent fry**	Density-independent survival rate	0.0001	Assumption	
	Migrant early summer 0+ from upstream to adults produced from migrant early summer 0+	Density-independent survival rate	0.001	Assumption	
	Migrant late summer 0+ juveniles from upstream to adults produced from late summer 0+ juveniles	Density-independent survival rate	0.005	Assumption	
	Spring 1+ smolts from upstream to adults produced from spring 1+	Density-independent survival rate	0.032	Chris Howard (2006, unpubl. data)	Survival based on ratio of returning adults to the estimate of smolts (from both branches/forks) two years prior, adults returning from WY 1997 to 2004.

Sub reach	Life-stage	Parameter	Value	Source	Comments
	smolts				

Appendix C

Chinook salmon population dynamics model parameters and values under current conditions in the Mill Creek Study Area.

Appendix C. Fall Chinook salmon population dynamics model parameters and values under current conditions in the Mill Creek Study Area.

Sub reach	Life-stage	Parameter	Value	Source	Comments
Initial population size	**Returning adults to mainstem Mill Creek to total female spawners**	Proportion of females	0.5	Waldvogel (2005)	Based on observed sex ratio of 1.1 to 1 (females to males) in the West Branch of Mill Creek, 1980 to 2002.
		Pre-spawning survival	0.8	Assumption	Pre-spawning survival assumed high, since Mill Creek is relatively low in the Smith River watershed.
		Proportion of female spawners to the West Branch	0.5	C. Howard (2006, unpubl. data)	Average fraction of spawner based on data from WY 1995 to 2005.
		Proportion of female spawners to the East Fork	0.5		
West Branch sub reach	**Female spawner to deposited eggs**	Suitable spawning gravel area	4840 m^2	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on densities of observed spawners and reconnaissance-level mapping of West Branch, 2005 field visit.
		Mean redd area	4.5 m^2	Burner (1951)	Mean redd area based on literature.
		Fecundity	3,900	Rowdy Creek Hatchery (1998, unpubl. data)	Assumed fecundity of 3,900 eggs/female based on Rowdy Creek Fish Hatchery data from WY 1994 to 1998.
	Deposited eggs to emergent fry	Survival rate	0.5	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on visual assessment of gravel quality observed during field reconnaissance visit in 2005.
	Emergent fry to 0+ smolts (> 55 mm)	Maximum fry density	0.6 fish/m^2	C. Howard (2006, unpubl. data)	Density and suitable habitat area parameterized to produce 6,000 0+ smolts, carrying capacity determined from graph of 0+ smolts versus emergent fry.
		Suitable habitat area	10,000 m^2		
		Density-independent survival rate	0.8	Assumption	Density-independent survival assumed to be high; mortality primarily due to density-dependent effects.
East Fork sub reach	**Female spawner to deposited eggs**	Suitable spawning gravel area	5360 m^2	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on densities of observed spawners and reconnaissance-level mapping of West Branch, 2005 field visit.
		Mean redd area	4.5 m^2	Burner (1951)	Mean redd area based on literature.
		Fecundity	3,900	Rowdy Creek Hatchery (1998, unpubl. data)	Assumed fecundity of 3,900 eggs/female based on Rowdy Creek Fish Hatchery data from WY 1994 to 1998.

Sub reach	Life-stage	Parameter	Value	Source	Comments
	Deposited eggs to emergent fry	Survival rate	0.1	Field reconnaissance data (Stillwater Sciences 2005, unpubl. data)	Based on visual assessment of gravel quality observed during field reconnaissance visit in 2005.
	Emergent fry to 0+ smolts (> 55 mm)	Maximum fry density	0.5 fish/m^2	C. Howard (2006, unpubl. data)	Density and suitable habitat area parameterized to produce 5,000 0+ smolts, carrying capacity determined from graph of 0+ smolts versus emergent fry.
		Suitable habitat area	10,000 m^2		
		Density-independent survival rate	0.8	Assumption	Density-independent survival assumed to be high; mortality primarily due to density-dependent effects.
Below West Branch and East Fork	**Migrant emergent fry from upstream to returning adults**	Density-independent survival rate	0.0001	Assumption	Survival assumed to be low.
	0+ smolts from upstream to returning adults	Density-independent survival rate	0.024	C. Howard (2006, unpubl. data)	Based on the ratio of 3-year old returning adults to number of 0+ smolts (>55 mm FL).

Appendix D

Model sensitivity analyses, coho salmon population model, Mill Creek.

Appendix D. Model sensitivity analyses, coho salmon population model, Mill Creek.

Table D-1. Based on current conditions.

Relation	Parameter	Parameter values					One-step responses					Steady-state responses				
Adults returning to Mill Creek to total female spawners	Proportion of Females	0.25	0.38	0.50	0.67	1.00	318	331	337	339	344	317	331	337	339	344
	Pre-spawning survival	0.50	0.75	1.00	1.33	2.00	318	331	337	339	344	317	331	337	339	344
Total female spawners to West Branch female spawners	Proportion of Spawners to West Branch	0.25	0.38	0.50	0.67	1.00	334	335	337	331	240	334	335	337	331	236
West Branch female spawners to deposited eggs	Suitable spawning gravel area (m²)	1505	2258	3010	4012	6020	336	337	337	337	337	336	337	337	337	337
	Mean redd area (m²)	1.40	2.10	2.80	3.73	5.60	337	337	337	337	336	337	337	337	337	336
	Fecundity (#eggs/female)	1150	1725	2300	3066	4600	333	335	337	339	344	333	335	337	339	344
West Branch, Deposited eggs to emergent fry	Density-independent survival	0.25	0.38	0.50	0.67	1.00	333	335	337	339	344	333	335	337	339	344
West Branch, Emergent fry to early summer 0+	Suitable habitat area (m²)	5000	7500	10000	13330	20000	298	317	337	363	414	297	317	337	363	416
	Density (fish/m²)	1.25	1.88	2.50	3.33	5.00	298	317	337	363	414	297	317	337	363	416
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	333	335	337	339	339	333	335	337	339	339
West Branch, Early summer 0+ to late summer 0+	Density-independent survival	0.40	0.60	0.80	1.07	1.60	297	317	337	357	357	296	316	337	357	357
West Branch, Late summer 0+ to spring 1+ smolts	Suitable habitat area (m²)	7900	11850	15800	21061	31600	262	299	337	387	486	257	299	337	388	490
	Density (fish/m²)	0.18	0.26	0.35	0.47	0.70	262	299	337	387	486	257	299	337	388	490
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	297	317	337	357	357	296	316	337	357	357
East Fork female spawners to deposited eggs	Suitable spawning gravel area (m²)	1670	2505	3340	4452	6680	337	337	337	337	337	337	337	337	337	337
	Mean redd area (m²)	1.40	2.10	2.80	3.73	5.60	337	337	337	337	337	337	337	337	337	337
	Fecundity (#eggs/female)	1150	1725	2300	3066	4600	321	332	337	337	338	319	332	337	337	338
East Fork, Deposited eggs to emergent fry	Density-independent survival	0.05	0.08	0.10	0.13	0.20	321	332	337	337	338	319	332	337	337	338
East Fork, Emergent fry to early summer 0+	Suitable habitat area (m²)	11850	17775	23700	31592	47400	318	327	337	344	344	318	327	337	345	345
	Density (fish/m²)	0.26	0.38	0.51	0.68	1.02	318	327	337	344	344	318	327	337	345	345
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	321	332	337	337	337	319	332	337	337	337
East Fork, Early summer 0+ to late summer 0+	Density-independent survival	0.40	0.60	0.80	1.07	1.60	317	327	337	346	346	317	327	337	347	347
East Fork, Late summer 0+ to spring 1+ smolts	Suitable habitat area (m²)	11850	17775	23700	31592	47400	305	321	337	358	401	304	320	337	359	402
	Density (fish/m²)	0.05	0.08	0.10	0.13	0.20	305	321	337	358	401	304	320	337	359	402
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	317	327	337	346	346	317	327	337	347	347
Below West Branch and East Fork, Migrant emergent fry from upstream to adults produced from emergent fry	Density-independent survival	0.0001	0.0001	0.0001	0.0001	0.0002	334	336	337	338	342	334	336	337	338	342
Below West Branch and East Fork, Migrant early summer 0+ from upstream to adults produced from migrant early summer 0+	Density-independent survival	0.0005	0.0008	0.0010	0.0013	0.0020	337	337	337	337	337	337	337	337	337	337
Below West Branch and East Fork, Migrant late summer 0+ juveniles from upstream to adults produced from late summer 0+ juveniles	Density-independent survival	0.0025	0.0038	0.0050	0.0067	0.0100	297	317	337	363	416	296	317	337	364	418
Below West Branch and East Fork, Spring 1+ smolts from upstream to adults produced from spring 1+ smolts	Density-independent survival	0.02	0.02	0.03	0.04	0.06	210	274	337	421	590	196	271	337	423	595

Appendix D. Model sensitivity analyses, coho salmon population model, Mill Creek.

Table D-2. Based on revised marine conditions (survival from 1+ smolt to adult of 0.006).

Relation	Parameter	Parameter values					One-step responses					Steady-state responses				
Adults returning to Mill Creek to total female spawners	Proportion of Females	0.25	0.38	0.50	0.67	1.00	29	42	55	71	101	0	0	55	109	125
	Pre-spawning survival	0.50	0.75	1.00	1.33	2.00	29	42	55	71	101	0	0	55	109	125
Total female spawners to West Branch female spawners	Proportion of Spawners to West Branch	0.25	0.38	0.50	0.67	1.00	38	47	55	64	83	0	0	55	97	87
West Branch female spawners to deposited eggs	Suitable spawning gravel area (m²)	1440	2160	2880	3839	5760	54	54	55	55	55	50	53	55	56	57
	Mean redd area (m²)	1.40	2.10	2.80	3.73	5.60	55	55	55	54	54	57	56	55	53	50
	Fecundity (#eggs/female)	1150	1725	2300	3066	4600	33	45	55	68	94	0	0	55	103	105
West Branch, Deposited eggs to emergent fry	Density-independent survival	0.25	0.38	0.50	0.67	1.00	33	45	55	68	94	0	0	55	103	105
West Branch, Emergent fry to early summer 0+	Suitable habitat area (m²)	5000	7500	10000	13330	20000	55	55	55	55	55	55	55	55	55	55
	Density (fish/m²)	1.25	1.88	2.50	3.33	5.00	55	55	55	55	55	55	55	55	55	55
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	33	45	55	64	64	0	0	55	103	103
West Branch, Early summer 0+ to late summer 0+	Density-independent survival	0.40	0.60	0.80	1.07	1.60	33	45	55	64	64	0	0	55	126	126
West Branch, Late summer 0+ to spring 1+ smolts	Suitable habitat area (m²)	7900	11850	15800	21061	31600	52	53	55	56	57	29	42	55	70	96
	Density (fish/m²)	0.18	0.26	0.35	0.47	0.70	52	53	55	56	57	29	42	55	70	96
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	33	45	55	64	64	0	0	55	126	126
East Fork female spawners to deposited eggs	Suitable spawning gravel area (m²)	1200	1800	2400	3199	4800	54	54	55	55	55	53	54	55	55	55
	Mean redd area (m²)	1.40	2.10	2.80	3.73	5.60	55	55	55	54	54	55	55	55	54	53
	Fecundity (#eggs/female)	1150	1725	2300	3066	4600	50	52	55	58	63	0	39	55	87	123
East Fork, Deposited eggs to emergent fry	Density-independent survival	0.05	0.08	0.10	0.13	0.20	50	52	55	58	63	0	39	55	87	123
East Fork, Emergent fry to early summer 0+	Suitable habitat area (m²)	11850	17775	23700	31592	47400	55	55	55	55	55	55	55	55	55	55
	Density (fish/m²)	0.26	0.38	0.51	0.68	1.02	55	55	55	55	55	55	55	55	55	55
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	50	52	55	57	57	0	39	55	79	79
East Fork, Early summer 0+ to late summer 0+	Density-independent survival	0.40	0.60	0.80	1.07	1.60	50	52	55	57	57	0	39	55	79	79
East Fork, Late summer 0+ to spring 1+ smolts	Suitable habitat area (m²)	11850	17775	23700	31592	47400	54	55	55	55	55	52	55	55	55	55
	Density (fish/m²)	0.05	0.08	0.10	0.13	0.20	54	55	55	55	55	52	55	55	55	55
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	50	52	55	57	57	0	39	55	79	79
Below West Branch and East Fork, Migrant emergent fry from upstream to adults produced from emergent fry	Density-independent survival	0.0001	0.0001	0.0001	0.0001	0.0002	55	55	55	55	55	55	55	55	55	55
Below West Branch and East Fork, Migrant early summer 0+ from upstream to adults produced from migrant early summer 0+	Density-independent survival	0.0005	0.0008	0.0010	0.0013	0.0020	55	55	55	55	55	55	55	55	55	55
Below West Branch and East Fork, Migrant late summer 0+ juveniles from upstream to adults produced from late summer 0+ juveniles	Density-independent survival	0.0025	0.0038	0.0050	0.0067	0.0100	49	52	55	59	66	42	44	55	125	180
Below West Branch and East Fork, Spring 1+ smolts from upstream to adults produced from spring 1+ smolts	Density-independent survival	0.00	0.00	0.01	0.01	0.01	33	44	55	69	97	0	0	55	121	158

Appendix E

Model sensitivity analysis, Chinook salmon population model, Mill Creek (based on current conditions).

Appendix E. Model sensitivity analysis, Chinook salmon population model, Mill Creek (based on current conditions).

Relation	Parameter	Parameter values					One-step responses					Steady-state responses				
Adults returning to Mill Creek to total female spawners	Proportion of Females	0.26	0.39	0.52	0.70	1.05	270	273	276	281	289	270	273	276	281	290
	Pre-spawning survival	0.50	0.75	1.00	1.33	2.00	270	273	276	281	289	270	273	276	281	290
Total female spawners to West Branch female spawners	Proportion of Spawners to West Branch	0.25	0.38	0.50	0.67	1.00	273	275	276	278	279	273	275	276	278	280
West Branch female spawners to deposited eggs	Suitable spawning gravel area (m^2)	2420	3630	4840	6452	9680	276	276	276	276	276	276	276	276	276	276
	Mean redd area (m^2)	2.25	3.38	4.50	6.00	9.00	276	276	276	276	276	276	276	276	276	276
	Fecundity (#eggs/female)	1950	2925	3900	5199	7800	271	274	276	280	288	271	274	276	280	289
West Branch, Deposited eggs to emergent fry	Density-independent survival	0.25	0.38	0.50	0.67	1.00	271	274	276	280	288	271	274	276	280	289
West Branch, Emergent fry to 0+ smolts	Suitable habitat area (m^2)	5000	7500	10000	13330	20000	205	241	276	324	420	201	239	276	327	427
	Density (fish/m^2)	0.30	0.45	0.60	0.80	1.20	205	241	276	324	420	201	239	276	327	427
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	271	274	276	279	279	271	274	276	279	279
East Fork female spawners to deposited eggs	Suitable spawning gravel area (m^2)	2680	4020	5360	7145	10720	276	276	276	276	276	276	276	276	276	276
	Mean redd area (m^2)	2.25	3.38	4.50	6.00	9.00	276	276	276	276	276	276	276	276	276	276
	Fecundity (#eggs/female)	1950	2925	3900	5199	7800	275	276	276	277	279	275	276	276	277	279
East Fork, Deposited eggs to emergent fry	Density-independent survival	0.05	0.08	0.10	0.13	0.20	275	276	276	277	279	275	276	276	277	279
East Fork, Emergent fry to 0+ smolts	Suitable habitat area (m^2)	5000	7500	10000	13330	20000	217	247	276	316	396	214	245	276	318	402
	Density (fish/m^2)	0.25	0.38	0.50	0.67	1.00	217	247	276	316	396	214	245	276	318	402
	Density-independent survival	0.40	0.60	0.80	1.07	1.60	275	276	276	277	277	275	276	276	277	277
Below West Branch and East Fork, Migrant emergent fry from upstream to returning adult	Ocean survival	0.0001	0.0001	0.0001	0.0001	0.0002	270	273	276	281	289	270	273	276	281	290
Below West Branch and East Fork, 0+ smolts from upstream to returning adult	Ocean survival	0.01	0.02	0.02	0.03	0.05	144	210	276	364	540	138	207	276	369	554